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STUDIES OF THE STAMINATE INFLORESCENCE AND POLLEN OF HICORIA PECAN[1]

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INTRODUCTION

From the producer's standpoint one of the most important limiting factors to profits in pecan culture is low yields. These may be due to any one or to a combination of several factors, such as the failure of the trees to differentiate flowers, more especially pistillate flowers, poor pollen, unfavorable weather during the flowering season, or insect or disease attack upon flowers or developing fruits. Considerable study has been devoted to some of these questions. Little, however, has been recorded regarding the development of pollen in the pecan, though pollen deficiencies are known to be responsible for unsatisfactory fruit setting in certain varieties of apples, pears, plums, grapes, and many other fruits. It therefore appeared to the writer that a study of the morphology of the staminate inflorescence and physiology of the pollen would throw some light on practical questions of pollination.

REVIEW OF LITERATURE

Unfruitfulness of the pecan (*Hicoria pecan* Brit.) is associated more closely with the initiation and development of pistillate than of staminate flowers, and it is therefore logical that the pistillate flowers should have been studied first. Studies of the morphology of pistillate flowers of pecans have been made by Woodroof (*27*, *28*),[3] Shuhart (*21*), and Isbell (*12*), and the results have shown close agreement as to the time and manner of development. Staminate flowers have received secondary attention, but fragmentary descriptions have appeared in a few reports (*23*, *26*, *12*, *27*, *28*).

Stuckey (*23*) studied the development of staminate flowers of 33 varieties of pecans. He divided the varieties into two groups on the basis of the length and size of the catkins, length of bracts, and time of shedding pollen. Woodroof (*26*, *27*) found that catkins were differentiated in lateral buds throughout the growing season of

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[2] In the investigations here reported Naomi C. Woodroof, of the Department of Botany, and J. E. Bailey, of the Department of Horticulture, of the Georgia Agricultural Experiment Station, aided in collecting field data and in preparing material for laboratory studies. Otis Woodard, of the Georgia Coastal Plain Experiment Station, furnished a part of the data for Table 5; C. F. Williams, of the North Carolina Agricultural Experiment Station, and R. M. Middleton, of the Georgia station, furnished a part of the data for the same table. Members of the Department of Horticulture of Michigan State College offered suggestions in the planning of the work and criticized the manuscript; and W. C. Dutton aided in making photomicrographs.

[3] Reference is made by number (italic) to "Literature cited," p. 1103.

the year prior to the shedding of pollen. He reported measurements of catkins of the two groups of varieties during the winter stage and described the method of shedding bud scales the following spring. Isbell (*12*) published 13 photomicrographs illustrating progressive stages of catkin development during the summer.

Higgins (*10*) described a disease (*Microstroma juglandis* (Bereng.) Sacc., var. *robustum*, n. var.) of pecan catkins that appeared on all of the varieties observed and sometimes destroyed one-third of the pollen. The tissues of the catkin were not killed outright, but the pollen grains degenerated, often leaving collapsed walls. This disease is common in the orchard in which the present studies were made, but care was taken to avoid using diseased material.

Schuster (*18*) stated that the amount of pollen produced by filberts in Oregon varies from season to season and is influenced by many factors. Many varieties produce a heavy crop of staminate and pistillate flowers one year, and a light crop of both the following year.

Valleau (*24*), working with strawberries, Dorsey (*8*) with plums, Knowlton (*15*) with the J. H. Hale peach, and Asami (*3*) with Shanghai peach, report that the first abnormal development in pollen was seen at the time of liberation from the tetrad wall; thereafter microspores were found in various stages of abortion. Shoemaker (*19*, *20*) found lagging chromosomes in the heterotypic division, giving rise to abnormal pollen in the apple and cherry.

The germination of pollen on artificial media has been unsatisfactorily accomplished with pollen of many plants. Wood [4] found that almond and walnut pollen did not germinate well on sugar-agar media, and concluded that there was no satisfactory laboratory method of ascertaining the viability of pollen of various varieties. Anthony and Harlan (*2*) attempted to duplicate natural conditions for germinating barley pollen by placing a piece of mesophyll from the leaf of the garden pea in the cell to supply water. The cell was covered with a cover glass and placed in the open to allow the condensation of moisture on the pollen grains. Germination was accomplished with both mesophyll and drops of water for humidifiers. Beaumont and Knight (*5*) and Knowlton (*15*) attempted to approach natural conditions for germinating apple pollen by adding stigmas of the same or different varieties to a hanging drop at the same time the pollen was added. They concluded that further improvement of the method of germination was necessary to produce pollen-tube length equal to that produced under natural conditions. Lidforss (*17*) reported that artificial media for germinating pollen must contain not only the essential nutritive substances but that it must not contain substances which prevent growth, especially mineral salts, as calcium.

The most satisfactory results, from pollen-germination tests in general, have been obtained by using from 1 to 2 per cent agar or gelatin and 5 to 20 per cent sucrose in the media. Howlett (*11*) used 10 per cent sucrose and 2 per cent agar; Beaumont and Knight (*5*) used 5 per cent sucrose and 1 per cent gelatin for germinating apple pollen; Booth (*6*) used 15 per cent sucrose and 1½ per cent gelatin for germinating plum pollen and 10 per cent sucrose and 5 per cent gelatin for germinating cherry pollen; Schuster (*18*) obtained best germination of filbert pollen in 12 to 15 per cent sucrose but observed bursting of

[4] WOOD, M. N. POLLEN STUDIES OF ALMOND AND WALNUT. 1917. (Master's thesis. University of California.)

pollen grains and tubes; Auchter (*4*) germinated apple pollen in distilled water; and Knight (*14*) increased apple-pollen germination by adding a trace of asparagine to the medium.

Valleau (*24*) determined the percentage of defective grains in strawberry pollen and reported that—

> lactic acid has the advantage over water or alcohol for this purpose as it is not volatile and seldom, if ever, breaks the pollen grains through osmotic pressure. It readily enters and expands the normal grains, while it leaves the aborted grains collapsed.

Dorsey (*8*) studied plum pollen and reported that the extent of pollen abortion in selected forms was determined partly from mounts in lactic acid and partly from stained sections. In Shoemaker's (*19*) work with apples lactic acid was employed to afford a liquid medium which would prevent bursting and germination of the pollen grains. Beaumont and Knight (*5*) hand-pollinated apple blossoms, and after the pollen had germinated and penetrated the stigmas the latter were flattened on a cover glass and mounted in lactic acid which killed and fixed the pollen tube. Snow (*22*) used lactic acid in a similar manner in studying the pollen of stocks. Florin's (*9*) germination tests closely checked with the lactic acid examinations of apple and pear pollen.

METHODS

Material for morphological studies was taken from an orchard of 28 varieties at the Georgia Experiment Station. The location is about 150 miles north of the center of pecan production in Georgia. Most of the trees are 20 years old and have had uniform culture. Data on pollen dissemination were taken in commercial orahards near Barnesville, Ga.

In general, the methods of collecting, killing, fixing, embedding, sectioning, and staining material for microscopical studies were the same as those described in previous reports (*27*, *28*, *31*).

The Alley and Frotscher varieties were chosen as typical of Groups 1 and 2, respectively, according to Stuckey's classification (*23*). Other varieties were repeatedly used to verify results. Juel's fixative [5] and picro-sulphurous acid [6] were used as killing and fixing agents, the latter giving the better results. Material was taken at 15-day intervals throughout the year from each variety, alternating the fixatives. Normal buds were selected from representative shoots, and normal flowers were taken from catkins typical of the variety. From the mother-cell stage until pollen shedding, catkins of the Stuart variety were collected daily; and during the reduction division, material of the Frotscher and Stuart varieties was collected at 3-hour intervals. Buds collected during the actively growing season were sectioned 5 microns in thickness. The hairy nature of winter buds rendered it difficult to section them sufficiently thin for cellular studies.

A modification of the smear method, as described by Kaufmann (*13*), was used to determine the number of tetrads per anther and the number of pollen grains per pollen sac. An anther in the tetrad stage was placed in a drop of water on a slide and thoroughly macerated with a needle. The tetrads separated from the anther wall and floated independently in the medium. After the fragments of the anther

[5] Juel's fixative: $ZnCl_2$, 2 gm.; acetic acid, 2 c. c.; alcohol, 95 per cent, 50 c. c.; distilled H_2O, 50 c. c.

[6] Picro-sulphurous acid: Sulphurous acid, 6 per cent, 10 c. c.; picric acid, 1½ gm.; alcohol, 75 per cent, 90 c. c.

wall were removed the tetrads were stained with eosin, covered with a cover glass, and examined under the high power of the microscope.

Dissemination of pollen was studied by catching pollen from the air on slides greased with vaseline, a method similar to that used by Waugh (*25*) for catching plum, pear, and apple pollen. Two yardsticks wrapped with cheesecloth and loosely bolted together made a convenient holder for 12 slides. About two-thirds of the length of each slide was exposed, the remainder being held firmly between the yardsticks. Three series of slides were mounted on a slender pole,

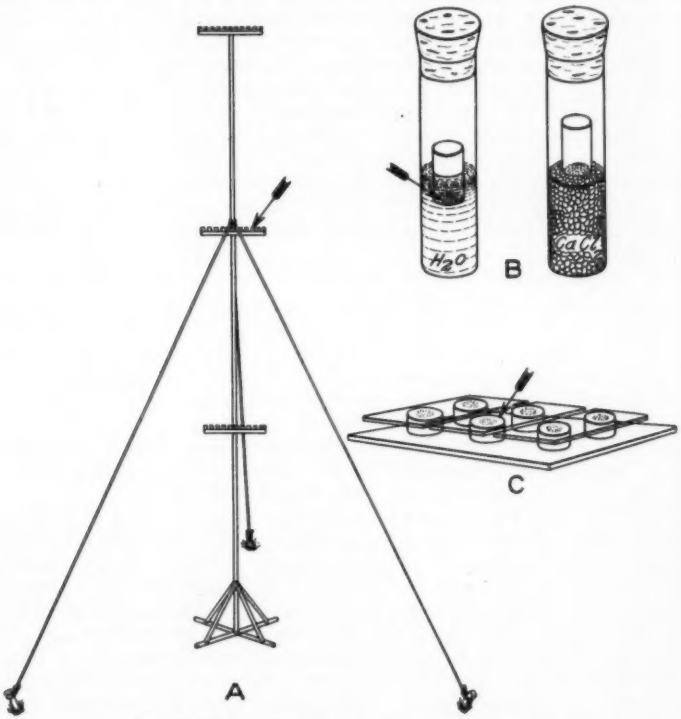

FIGURE 1.—A, Pole 30 feet high supported by guy wires to which were attached three series of greased slides for catching pollen from the air; B, vials containing water and calcium chloride, in which were placed smaller vials containing pecan pollen which was kept "moist" and "dry" respectively; C, cells for germinating pollen. Arrows in each case indicate position of the pollen

one series each 10, 20, and 30 feet above the ground. The slides were set on the leeward side of the trees, at a 45° angle with the ground, the greased face of the slide being turned toward the pollen-shedding trees. The slides were changed by lowering and raising the pole with three guy wires. (Fig. 1, A.)

Pecan pollen grains on the greased slides were identified and counted under the low-power objective of the microscope. After the area of the microscopical field was calculated, the number of grains in 200 fields were counted, averaged, and calculated to the number of grains per square centimeter.

The wind velocity was determined by the use of a Robinson cup anemometer with electric connections and a buzzer which indicated the number of miles per hour. The relative humidity was determined by the use of a stationary hygrometer placed in the orchard.

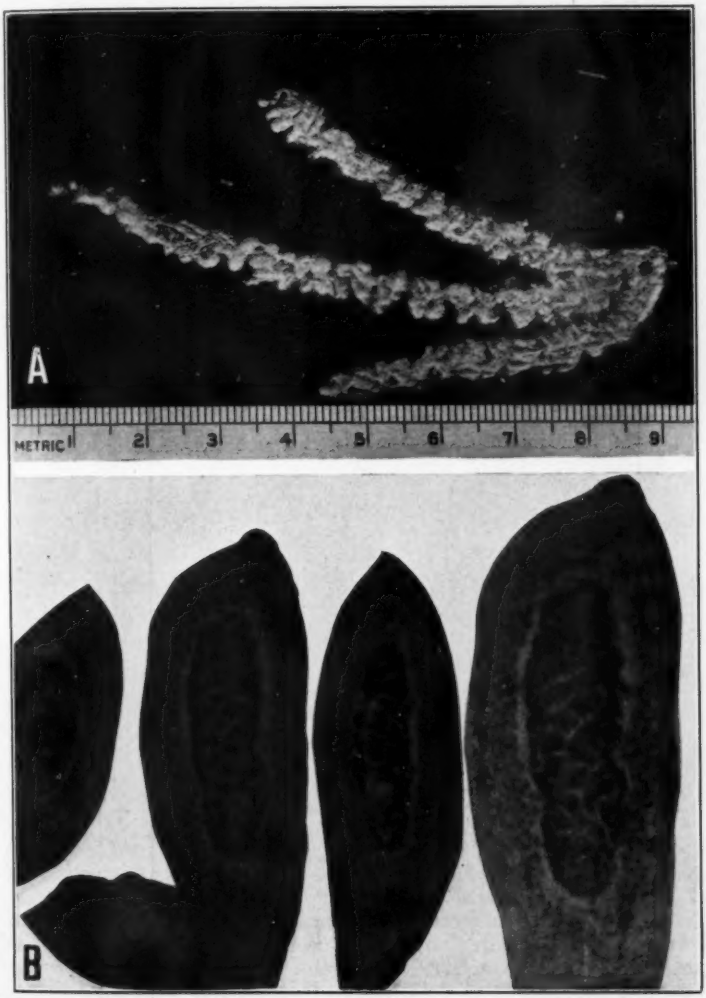

FIGURE 2.—A, Microspore print made from a pecan catkin of Group 1 showing the ease with which pecan pollen may be collected in quantity; B, photomicrograph of longitudinal section of Alley variety anther while in the mother-cell stage on April 1; in some cases there seem to be rows of mother cells

Pollen for germination tests was obtained from ripe anthers which were allowed to dehisce in the laboratory. (Fig. 2.) In this way the time of dehiscence could be determined to within two hours. Cells for germinating pollen were made by shellacking six hard

rubber rings, 15 mm. in diameter and 10 mm. high, to glass slides 2 inches wide and 3 inches long. Water to supply moisture for germination was placed in the bottom of each cell. A drop of sterile germinating medium was placed on a cover glass while hot and allowed to solidify. The pollen was dusted on the medium and the cover glass was inverted and sealed on the cell with vaseline. Examinations were made at intervals under low power without disturbing the cell. (Fig. 1, C.)

Dry and moist storage conditions were provided by placing calcium chloride and water, respectively, in two 50 c. c. vials. A 10 c. c. vial containing pollen was placed in each 50 c. c. vial and the latter was corked. (Fig. 1, B.) A duplicate series was set up for each variety and temperature. Electric ovens provided tempera-

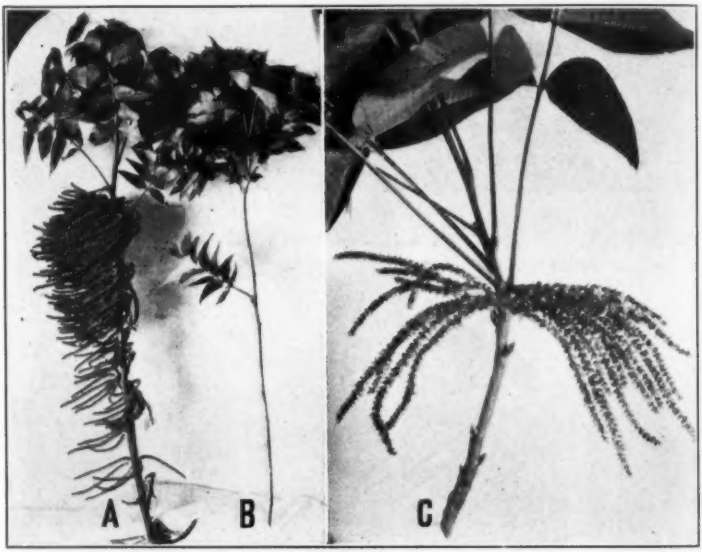

FIGURE 3.—A, Twig from Stuart pecan tree which bore 3 pounds of nuts last year; B, twig from Mobile tree which bore 29 pounds of nuts last year. This tree and that in A are both 12 years old and have received the same fertilizer and cultural treatments since being set in the orchard. C, Twig from McAlister variety, a supposed hybrid between *Hicoria pecan* and *Carya alba*, which has a catkin producing habit like *C. alba*, i. e., only the terminal bud produces catkins

tures constant at 32°, 25°, 23°, and 22° C.; and a refrigerator provided a temperature of 5° C.

Mounting pollen in lactic acid for microscopical determination of the percentage of defective grains seems a more reliable method than germinating it on artificial media. Two drops of 90 per cent lactic acid placed on a slide with a small amount of pollen and covered with a cover glass render the grains containing a normal amount of protoplasm distinct from those containing less than the normal amount. About three minutes are required for complete penetration; after three hours the grains become bleached and differentiation of defective and normal grains is uncertain. Fresh mounts and high magnification are necessary for one to make reliable counts by this method.

PRESENTATION OF EXPERIMENTAL DATA

The lateral buds of a growing shoot on a bearing pecan tree differentiate catkin primordia by the time the subtending leaf is one-tenth grown (*26*, *27*). Differentiation begins about two weeks after active growth starts in the spring (April 15) and continues throughout the growing season. In the pecan, catkins are always produced in lateral, axillary buds (figs. 3, 4), and the number of catkin primordia formed is in proportion to the number of leaves produced on that shoot. Normally there are two groups of three catkins each produced at each node. In other native hickories (*Carya alba*, *C. ovalis*, *C. glabra*) the catkins are produced in the terminal bud. (Fig. 3, C.)

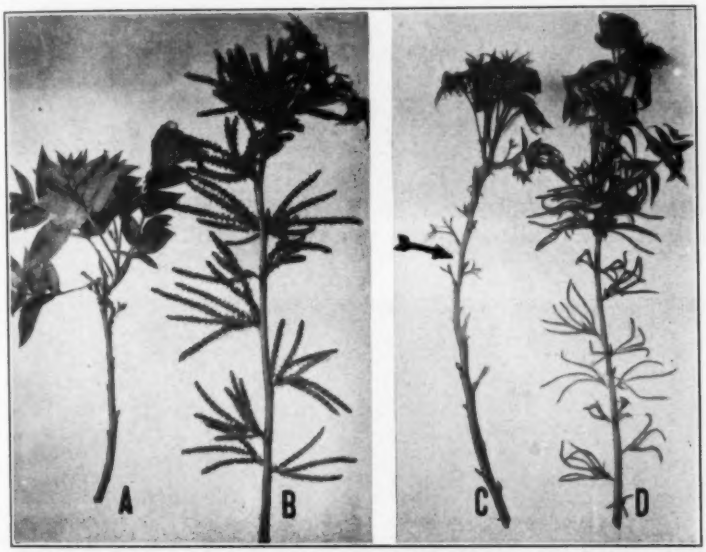

FIGURE 4.—A, Twig from Mobile tree which bore 58 pounds of nuts last year; tree from variety of Group 1; B, twig from Alley tree which bore 34 pounds of nuts last year; tree from variety of Group 1; C, twig from Frotscher variety which bore 100 pounds of nuts last year; tree from variety of Group 2; D, twig from Stuart tree which bore no nuts last year; tree from variety of Group 2. All of these trees are 20 years old and have received the same fertilizer and cultural treatments since being set. Arrow indicates point of abscission of the catkin buds on April 9

The characteristics of the buds and inclosed catkin primordia have been previously described by the writer (*26*). The central catkin is formed and develops somewhat in advance of the catkins borne on either side, and ultimately reaches a greater length at maturity. (Figs. 5, 6, 4.)

THE TWO GROUPS OF VARIETIES

Stuckey's (*23*) description of the two groups of varieties was based on characteristics of the catkins at the time of pollen shedding. The writer (*26*) found that the catkin primordia of Group 1 have a greater diameter and lesser length than those of Group 2 in both October and January (*26*). Such measurements aid in differentiating the

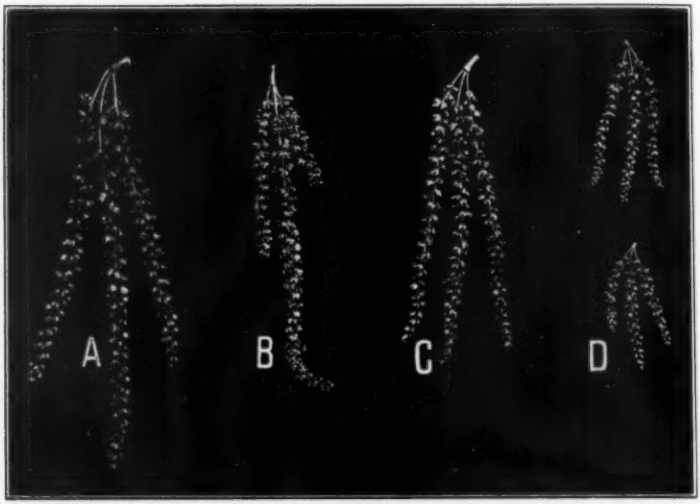

FIGURE 5.—Catkins of pecan varieties in Group 1: A, Alley; B, Jerome; C, Mobile; D, Mobile from nonvigorous bud (0.57 natural size)

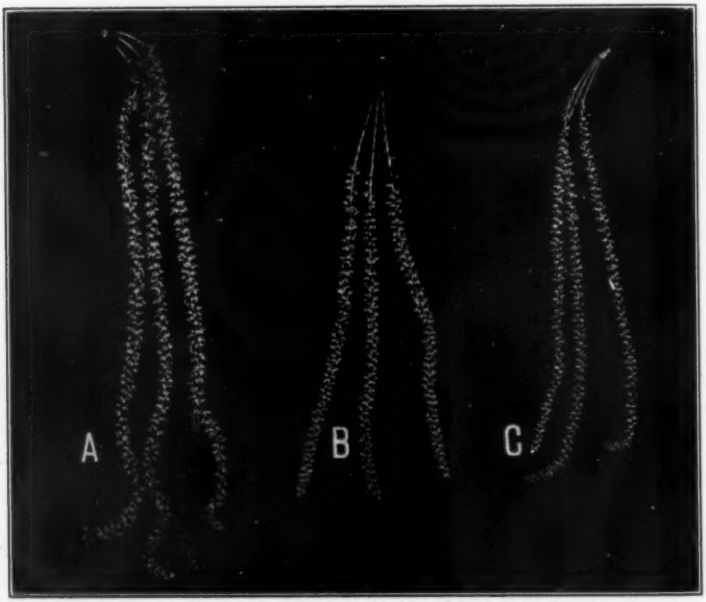

FIGURE 6.—Catkins of pecan varieties in Group 2: A, Van Deman; B, Frotscher; C, Teche. The Frotscher and Teche varieties have a large number of aborted flowers near the base of the cluster (0.57 natural size)

two groups, but as diameter and length vary with the vigor of the tree, they can not be depended upon solely.

There seems to be no difference between the mode of differentiation and type of growth of the catkins of the two groups of varieties during the spring and summer, but a marked difference is evident by early fall.

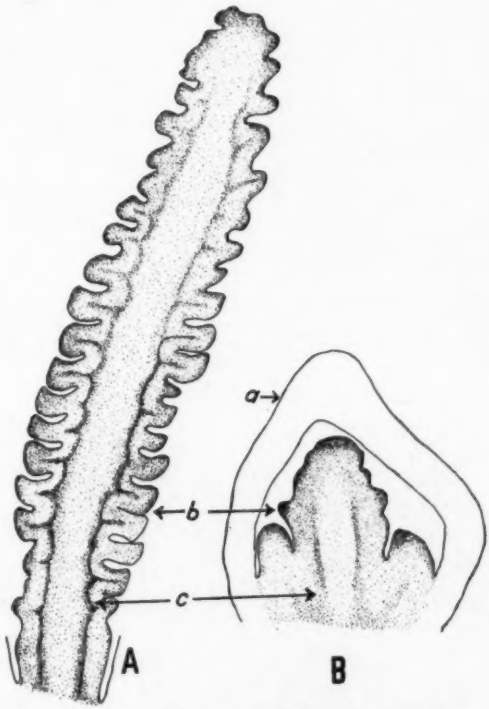

FIGURE 7.—Primordia of staminate inflorescence: B, Initial formation of a group of three catkins within a single bud scale, May 15; A, single inflorescence six weeks later: *a*, bud scale; *b*, primordium of an individual flower; *c*, initial formation of vascular bundles. Frotscher variety. × 181

Individual flower primordia develop as lateral "bumps" on the axis of the catkin primordium, beginning at the base and progressing toward the terminus. (Fig. 7.) In Group 1 flower primordia continue to form at the terminus, while the older ones near the base differentiate anthers by early fall. By the time growth practically ceases in the fall anthers are distinguishable along the entire length of the axis. (Figs. 8 and 9 and Table 1.) Thus the winter stage of Group 1 shows complete differentiation of anthers and bracts.

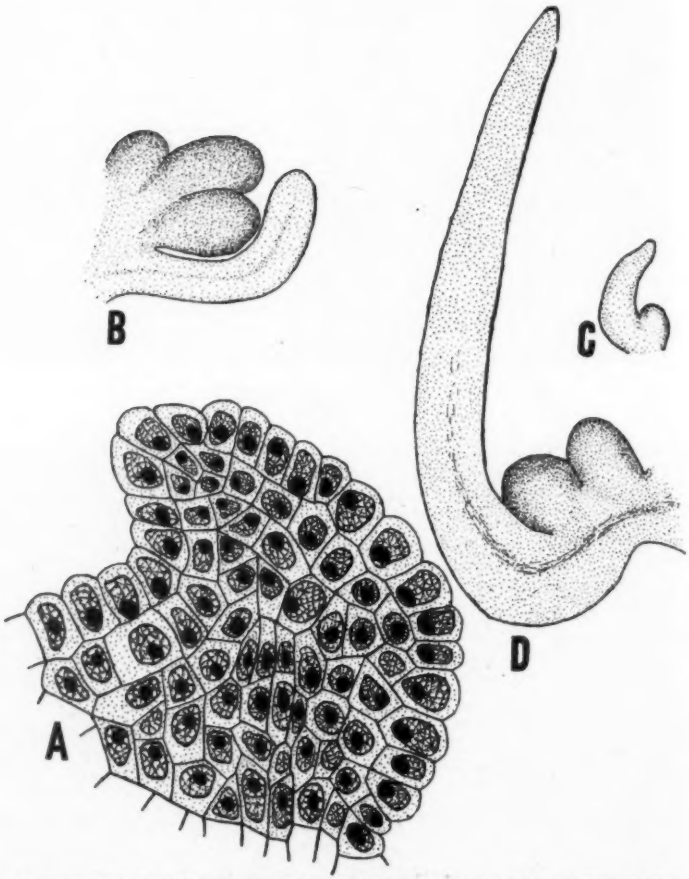

FIGURE 8.—A, Individual flower primordium showing specialization of cells but no differentiation of floral organs; enlargement of Figure 7, × 1040; B, Alley variety on March 15 showing floral organs well differentiated; × 114; C, Frotscher variety on March 15 showing very early stage in differentiation of floral organs; × 114; D, Frotscher variety on April 1 showing floral organs in same stage as Alley on March 15; × 114

FIGURE 9.—A, Photomicrograph of longitudinal section of two lobes of an anther showing mother cells just before rounding up; B, photomicrograph cross section of one lobe of an anther showing mother cells undergoing reduction division; C, photomicrograph cross section of one lobe of anther showing tapetum cells disintegrating, and tetrads within the mother cell walls; one tetrad is elongated, indicating abnormality

TABLE 1.—*Stages of development of pollen of pecan varities in Groups 1 and 2*

Stage of development	Groups at stage of development mentioned at time indicated																
	April	May	June	July	August	September	October	February	March			April			May		
									1	10	20	1	10	20	1	10
Differentiation of inflorescence	1, 2	1, 2	1, 2	1, 2	1, 2	1, 2											
Differentiation of anthers						1	1	2	2	2							
Formation of anther lobes										1	1, 2	2					
Archesporial cells										1	1, 2	2					
Mother cells											1	1, 2	2				
Rounding-up of mother cells											1	1, 2	2				
Reduction division											1	1, 2	2				
Tetrads												1	1, 2	2			
Microspore liberation												1	1, 2	2			
Anther dehiscence														1	1, 2		2

In Group 2 the flower primordia continue to form as long as growth continues in the fall, but no differentiation of anthers occurs

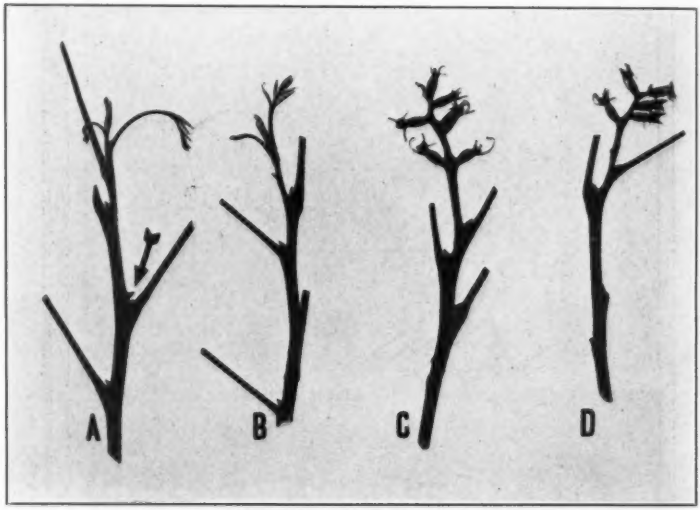

FIGURE 10.—Unfruitful (A, B) and fruitful (C, D) twigs; the auxiliary buds on both types of shoots produce staminate flowers the following spring (0.48 natural size)

until the following spring. Thus the individual flower primordia reach an inactive stage soon after formation and remain so for from four to nine months, while additional flower primordia continue formation toward the actively growing terminus. (Fig. 7.) Thus catkins of varieties of Group 2 are longer than those of Group 1. The period of inactivity varies with the time of formation—the basal and first-formed ones remain inactive longer than the newly formed terminal ones; also those formed in buds near the base of the new shoot early in the season are inactive for a longer time than those toward the terminus of the shoot. (Fig. 10.)

From early fall until the anthers are mature the following spring the development of the catkin primordia and the catkins of Group 1 is considerably in advance of that of Group 2. In the fall the difference is from 2 to 3 weeks; in winter when growth is almost at a standstill the maximum difference of 3 or 4 months occurs; while in spring when growth is most rapid the difference is from 10 to 15 days (figs. 4, 5, 6, and 11), and under some seasonal conditions the shedding of pollen of the two groups may be nearly coincident. (Table 5.)

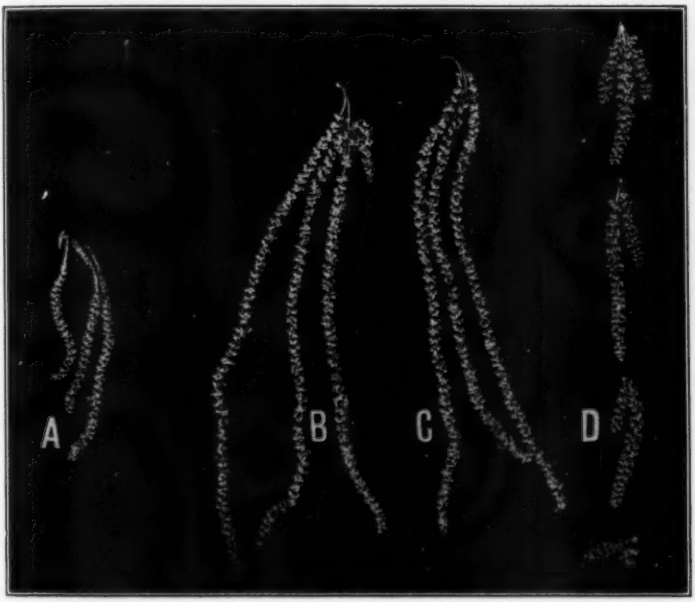

FIGURE 11.—A, Weak catkins with aborted flowers at base; B, vigorous catkins branched at base; C, normal catkin; D, aborted flowers from weak shoots. Indiana variety. (0.55 natural size)

The varieties of pecans can be separated into two groups in winter on the basis of the internal appearance of the lateral buds. Carefully cut and stained free-hand sections are sufficient to enable one to make the distinction. Practical use has been made of this fact in determining in advance the approximate date on which pollen of a new or unknown variety should shed.

The practical significance of the time of pollen shedding of the two groups will be discussed later. Anthers of varieties of Group 1 are differentiated several months before pollen shedding and differentiation occurs during the previous growing season, while differentiation of anthers of varieties of Group 2 occurs about two months before pollen shedding and takes place during the current growing season, as is the case with pistillate flowers (*28, 21, 12*). A closer relation thus exists in respect to time of differentiation between staminate and pistillate flowers of Group 2 than between staminate and pistillate flowers of Group 1.

INFLORESCENCE

A catkin primordium consists of three regions.

(1) The interior region occupies, as seen in longitudinal section, almost one-half of the diameter of the primordium. It consists entirely of large, slightly elongated, parenchyma cells, extending longitudinally with the axis. These remain parenchyma cells throughout the life of the catkin and are analogous to pith cells in a young shoot. The diameter of the spherical nuclei is about one-third the smallest diameter of the cell. The nuclei and cytoplasm do not stain as heavily as in the parenchyma cells of the primordia of individual flowers.

(2) Surrounding the interior region is a cylinder of small, narrow cells, with elongated nuclei which more than half fill the cells. The outline of this region is slightly irregular in both cross and longitudinal sections. In longitudinal section the cells vary greatly in size and shape and lie very close together. As growth continues these cells become sclerenchyma cells of the vascular bundles which connect each flower with the vascular system of the catkin.

(3) The third region of the catkin primordium consists of individual flower primordia which are made up entirely of parenchyma cells from the time of differentiation until September. (Fig. 8, A.)

In longitudinal section the epidermal cells of the flower primordium are rounded, uniform in size, but somewhat elongated. They lie close to one another and form a complete layer one cell thick over the surface. Directly beneath the epidermal layer are closely appressed 3-sided to 6-sided meristematic cells which vary widely in size. Sections made from material collected August 1 show that some of these cells are several times larger than others and are in a state of division. In the center of a flower primordium are several layers of elongated cells with oblong nucleii. These become sclerenchyma cells of a vascular system connecting each bract and anther with the vascular system of the catkin.

Bracts are differentiated about 10 days before the anthers. The first appearance of the bracts is shown by a turning of the terminus of the flower primordia toward the terminus of the catkin primordium, forming an angle of about 45°. As growth continues the bend becomes less abrupt and a protrusion appears in the axil. This protrusion divides immediately into four or five smaller ones, and each of these becomes an anther. (Figs. 8, 7.)

The development of bracts in spring is very rapid. Three branches soon form, the middle one being broader and longer than those on either side. The three almost envelop the developing anthers. (Figs. 6, 12.) The bracts contain chlorophyll, have numerous hairs on their surfaces and small veins, and presumably function as true leaves.

ANTHER

The anthers of the Frotscher variety on March 5 (40 days before shedding pollen) were a homogeneous mass of parenchyma cells covered by an epidermis. (Fig. 13, B.) Very early the anther appeared 4-lobed in cross section (fig. 14, B); and the differentiation of the vascular strand of the connective tissue outlined the general plan of structure. Almost simultaneously with the formation of lobes, a plate of hypodermal (archesporial) cells became differentiated in each lobe,

faintly distinguished from the adjacent cells by their large size, numerous sides, large nucleii, and less dense staining.

Subsequent divisions up to the mother-cell stage follow one another very rapidly. The archesporial cells divide by periclinal walls, form-

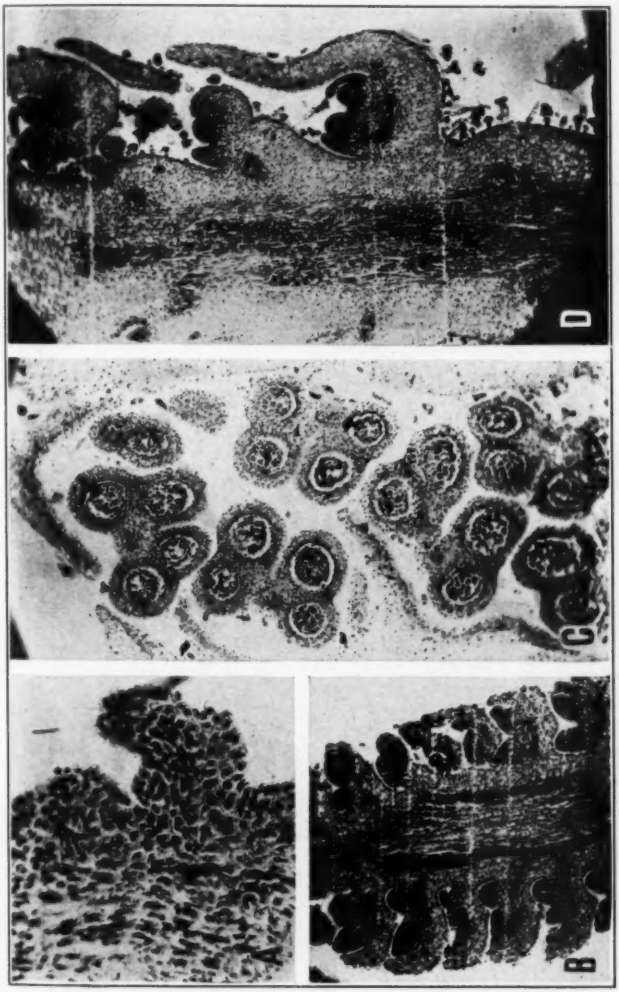

FIGURE 12.—Photomicrographs showing condition of flowers of Groups 1 and 2 on two different dates: A, Individual flower primordium just before differentiation of anthers, Group 2, Frotscher variety, December 1; B, longitudinal section of a catkin showing anthers formed in the Alley variety on December 1 as is typical of varieties in Group 1; C, cross section of several anthers showing tapetum cells broken down and mother cells separating, Alley variety, Group 1, April 1; D, longitudinal section of flowers of Frotscher variety, Group 2, on April 1, showing the anthers not yet differentiated into lobes

ing an outer layer of primary parietal (primary tapetum) cells, and an inner layer of primary sporogenous cells; the former producing the wall of the embedded sporangium and the latter the sporogenous tissue. The primary tapetum cells successively divide by periclinal walls until six or seven layers are formed. The inner layer is known

as the endothecium or tapetum, the outer layer as the exothecium or epidermis, the three or four remaining layers as "middle layers." The exothecium cells are thin walled, large and cubical, with large vacuoles and small oval nuclei which adhere to the sides of the cells toward the center of the anther. The cells of the middle layer are much smaller, somewhat compressed, many-sided, thin-walled, contain no vacuoles, have nuclei centrally located, are elongated, and

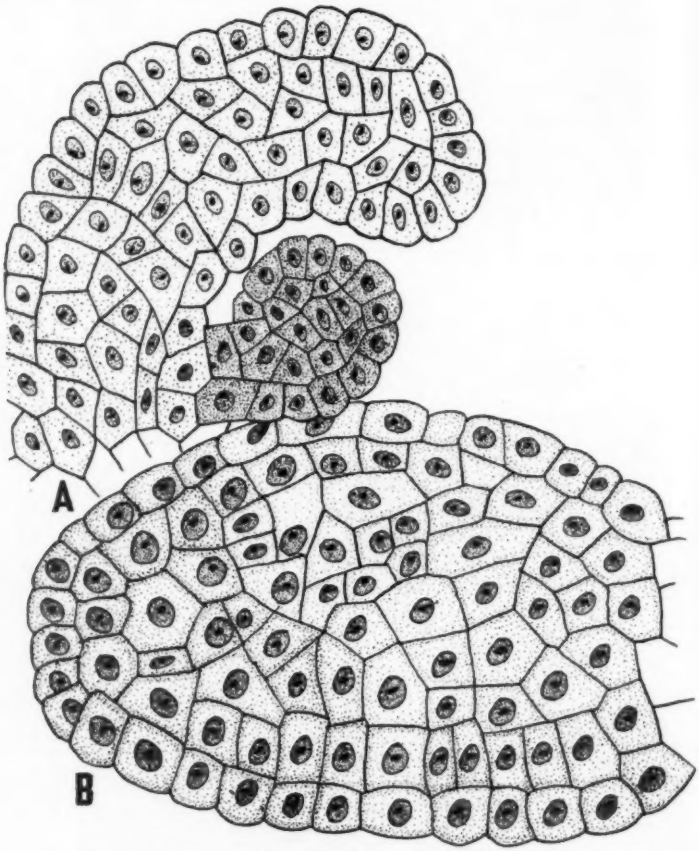

FIGURE 13.—Enlargements of Figure 8: A, Figure 8, C × 1,000; B, Figure 8, B × 1,000

stain lightly. The thick-walled, deeply staining, 6-sided, closely pressed, small nucleate tapetum cells form a jacket about the sporogenous cells, one or two cells in thickness.

Simultaneously with the division of the primary tapetum cells the primary sporogenous cells multiply without definite order to form mother cells. Division apparently occurs in every direction with occasional formation of layers but no definite massulae. Longitudi-

nally, the mass of closely compressed, many-sided, large nucleate mother cells extends almost the length of the anther, and about three cells wide. (Fig. 15, B.) They stain about as deeply as the middle layers but much lighter than the surrounding tapetum cells.

Further development is accompanied by separation, disorganization and disintegration of tapetum cells; and separation, increase in

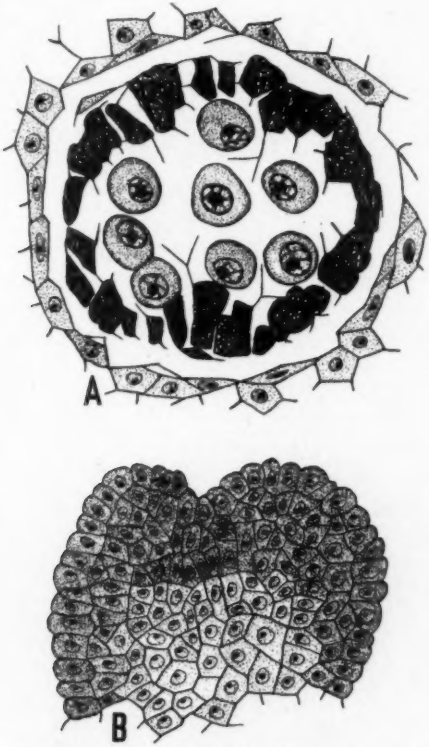

FIGURE 14.—A, Camera lucida drawing of cross section of an anther of Alley variety on April 5, showing rounding-up stage of the mother cells and continued disintegration of the tapetum cells; × 410: B, cross section of an anther of Frotscher variety on April 5, showing lack of differentiation of the interior into typical tapetum and mother cells; × 410

size, increase in thickness of walls, and rounding-up of the mother cells. (Figs. 14 and 16.)

The first evidence of disintegration of the tapetum cells occurs about 35 days before pollen shedding. (Fig. 15, B.) The layer of cells adjacent to the mother cells undergoes nuclear division once or twice, withdraws from the mother cells, shrinks in size, and clusters around the mother cells in a deeply staining irregular mass. Disintegration of the tapetum layer is increasingly rapid for 15 days, after which disintegration is almost complete and the fragments form an

incomplete layer around the mother cells. The layers of cells adjacent to the tapetum undergo similar but less rapid disintegration. These cells lose their contents and the walls collect around the periphery of the pollen sac. (Fig. 17.) The epidermis and the layer

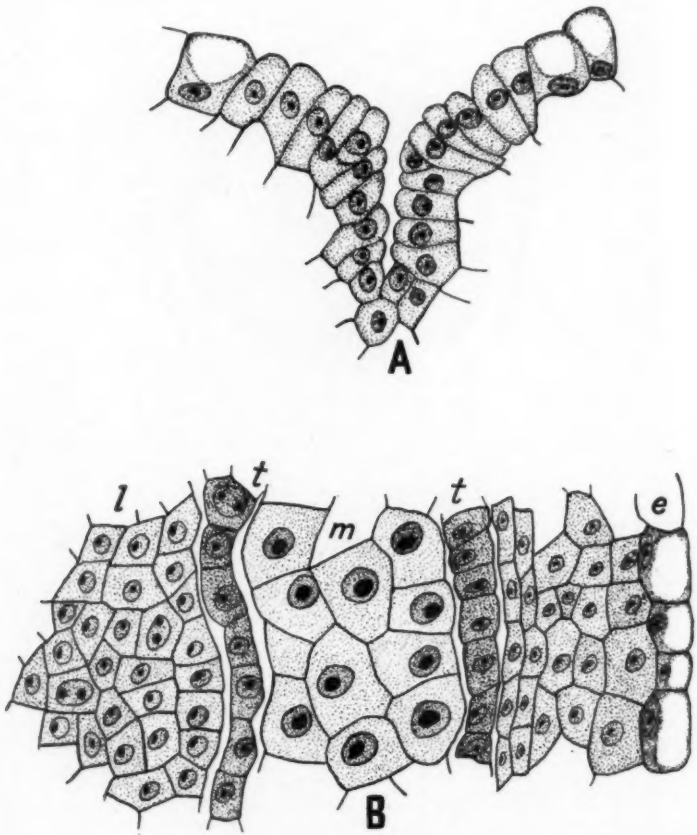

FIGURE 15.—A, Camera lucida drawing of cross section of a stomium of a mature anther; B, longitudinal section of a microsporangium showing the mature mother cells, *m*, just before rounding up; the tapetum cells, *t*, showing the first signs of disintegration; the cells between the loculi, *l*, and the epidermis, *e*

of cells next to it do not disintegrate, but increase in radial diameter. The cells of the middle layers continue to disintegrate until the pollen is mature and the wasting away of the wall separating two loculi on either side of the anther allows them to fuse into one, and is a part of the process of dehiscence.

The mother cells do not increase in number after the tapetum cells reach full size (35 to 40 days before pollen shedding). As the tapetum cells disintegrate, the mother cells become separated and loosely fill

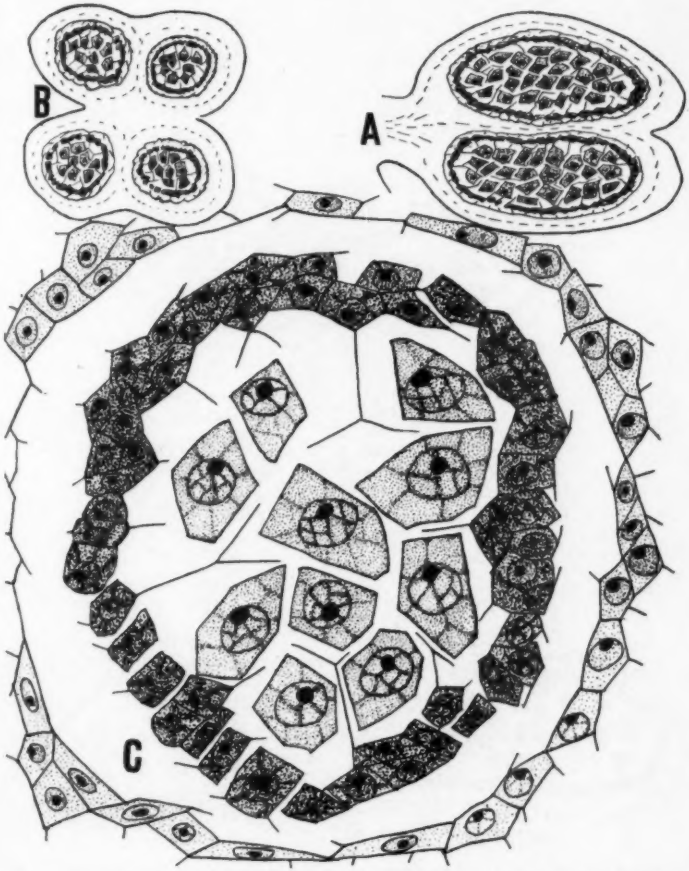

FIGURE 16.—A, Camera lucida drawing of longitudinal section of an anther of the Alley variety on April 1 showing the mother cells breaking apart and the tapetum cells rapidly disintegrating, × 110; B, A shown in cross section; × 110; C, enlargement of A; × 1003. The Frotscher variety reached this same stage on April 15

the sporangium. Rounding up occurs about 21 days before pollen shedding and reduction division follows immediately.

Division of the mother cells and formation of tetrads apparently require only a few hours and the entire process seems to go to completion in an anther at a specific time on a single day. (Fig. 18.)

TETRAD

It is during the heterotypic and homotypic divisions that the first abnormal behavior has been observed. The appearance of all of the mother cells is normal, and they seem very uniform in cell contents, staining reaction, and size and shape. (Figs. 2, 14, and 19.) In the process of division various types of abnormalities occur. Dividing cells were found in the Frotscher variety April 26 at 9 a. m. Practically all steps in the process of heterotypic and homotypic divisions were present in a single anther. In the formation of new nuclei the organization of the chromatin results in nuclei of various sizes and

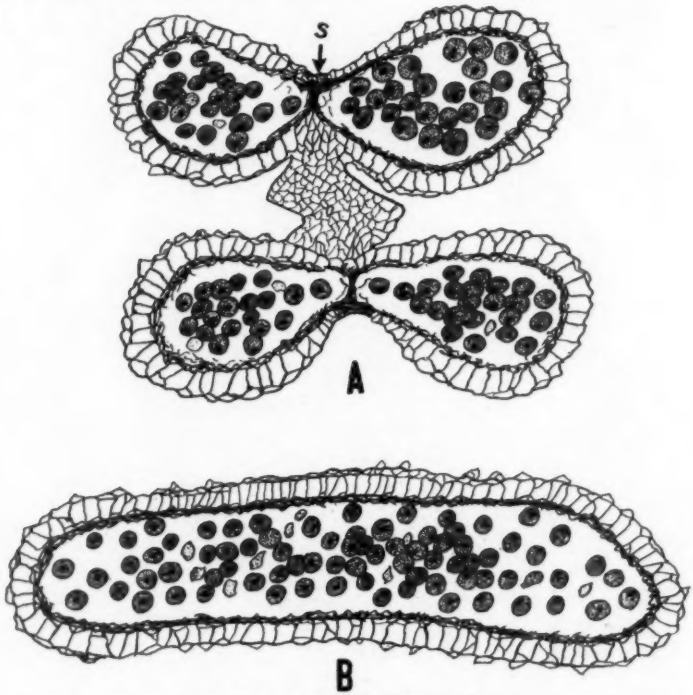

FIGURE 17.—Camera lucida drawing of cross section of anther just before dehiscence (A), and a tangential longitudinal section of the same (B); stomium at *s*. Stuart variety, May 13. × 110

density as determined by the intensity of staining. Because of the minuteness of the chromosomes the number has not been definitely determined. In most cases the haploid number was found to be 12, in others only 10. In some cases where the nucleus was in the anaphase stage of the first division, one or two chromosomes were lagging slightly, but in some of the more advanced stages they had completely caught up with the other chromosomes.

Both the successive and simultaneous methods of division of the mother cells are common in pecans, producing bilateral and tetrahedral arrangements, respectively, of the microspores. (Figs. 20, and 21.) In the bilateral arrangement the spindles lie in the same or

in perpendicular planes, and no wall is formed between the successive divisions. The two arrangements are about equally common. No case has been observed where the four microspores were in a row within the tetrad wall, nor has a failure of four microspores to form been found. Small supernumerary microspores are often seen which, according to Shoemaker (*19*), may be the result of small nuclei formed from lagging chromosomes, or, according to Coulter and Chamberlain (*7*), from division of one or more members of the tetrad. Small microspores are especially numerous in lots of pollen containing a

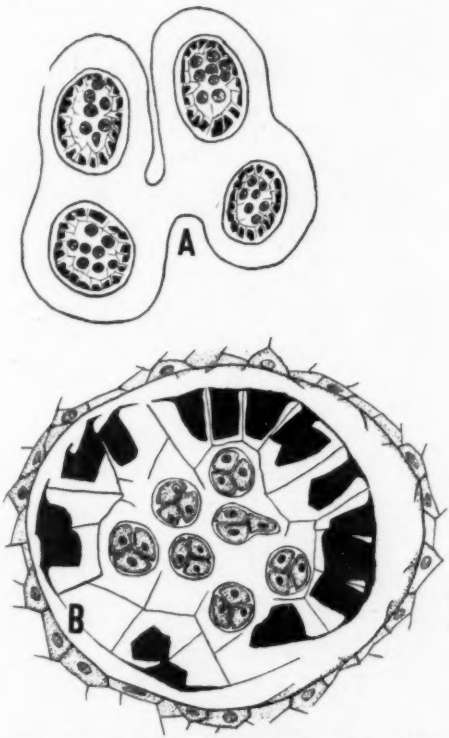

FIGURE 18.—A, Camera lucida drawing of cross section of an anther of the Frotscher variety on April 26 showing the tetrad stage with fragments of the tapetum cells; × 82; B, enlargement of A; × 400. Alley reached this stage on April 10

high percentage of defective grains and are almost always partially or totally void of cell contents. A few oversized grains were found, and the cell contents of most of them appeared normal. The normal number of pores is three, and variance is very rare with normal or undersized microspores; however, oversized microspores often have five or six pores.

At maturity some of the microspores are without nuclei and others without either nuclei or cytoplasm. The lack of protoplasmic contents is the basis of the lactic acid method of determining the percent-

age of defective pollen. By the use of this method defective grains were found in all lots examined, the number ranging from 0.3 to 81.7 per cent.

Flowers of the Beverage variety were found in the tetrad stage on April 24, and counts were made as follows: Four anthers taken from the base of a catkin contained 294, 373, 331, and 357 tetrads, respectively; and four anthers taken from the middle of the catkin contained 380, 380, 317, and 488 tetrads. Since each anther contains four pollen sacs, and each tetrad contains four microspores, the above figures also

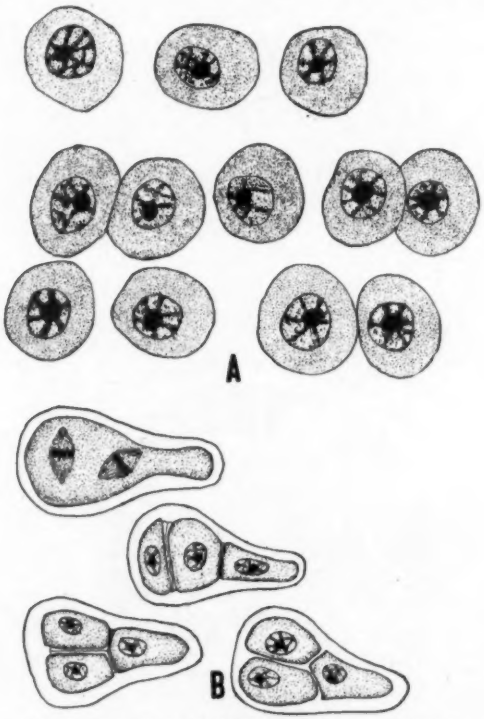

FIGURE 19.—A, Camera lucida drawing of mature mother cells that appear normal; B, mother cells with abnormal microspores. × 850

represent the average number of pollen grains per pollen sac in the respective anthers, the general average being 365.

Liberation of the microspores (pollen grains) occurs from 15 to 20 days before the pollen is shed. Because of the disintegration of the tapetum and surrounding cells, the pollen sac is only partially filled with pollen. Upon liberation from the tetrad wall the grains wander independently within the pollen sac and rapidly enlarge in size, but as the cavity continues to enlarge, owing to the continued disintegration of the surrounding sterile cells, the pollen sac remains only partially filled.

DEHISCENCE OF ANTHERS

The fusion of the four pollen sacs into two loculi by the dissolution of the separating wall occurs only a few days before the opening of

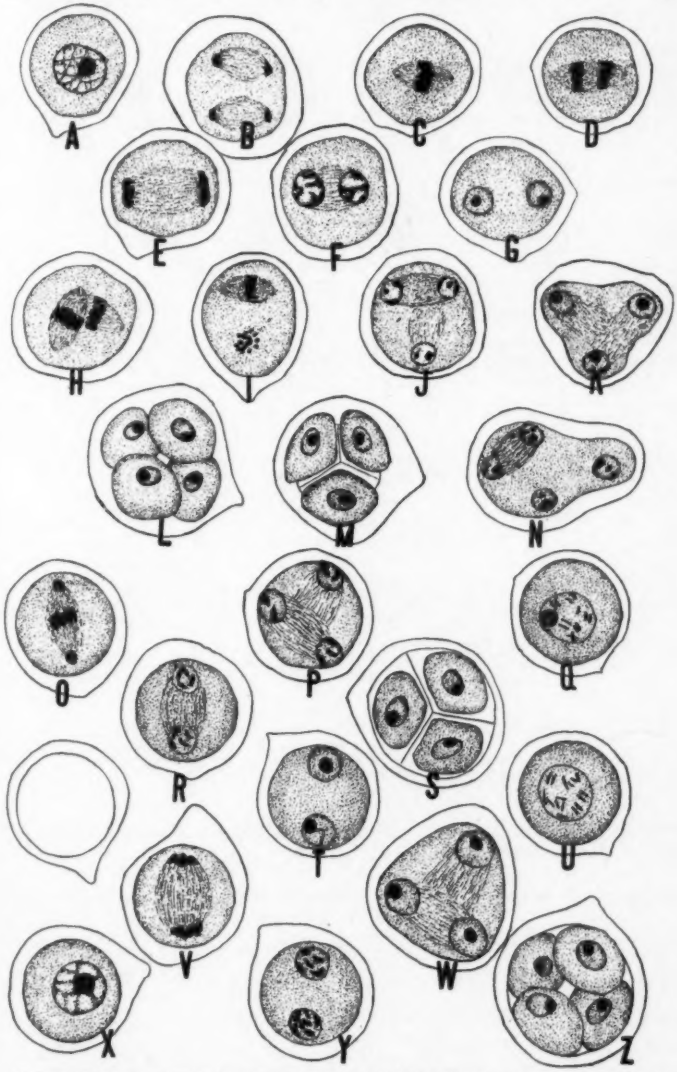

FIGURE 20.—Camera lucida drawings of stages of divisions of pollen mother cells at 9 a. m., April 26; Frotscher variety. Note formation of both bilateral and tetrahedral arrangements of microspores; all had reached the tetrad stage the following day. × 850

the anther on either side by means of a stomium, with consequent liberation of pollen grains at maturity. (Figs. 15 and 17.) The anther wall is two cells thick, with fragments of one or more additional

layers. The opening of the anther is due to drying of the exterior or epidermal cells and consequent contraction of the outer in proportion to the inner surface. Reclosing of anthers occurs when moisture is

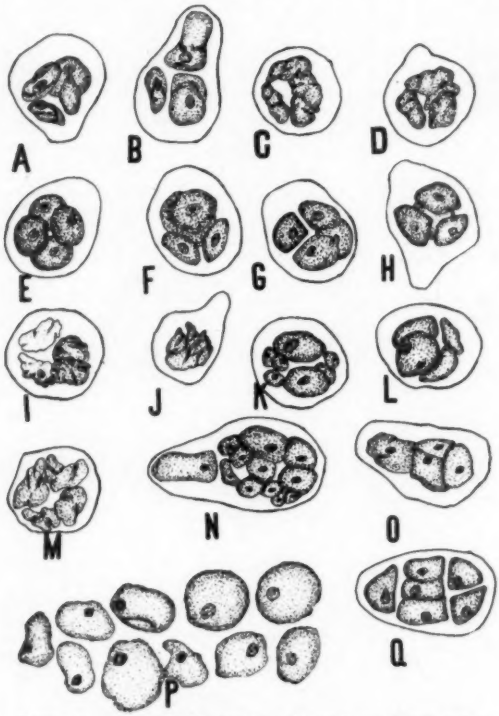

FIGURE 21.—Camera lucida drawings of tetrads and young pollen grains: E, F, G, and H appear normal; K, N, and Q contain more than four microspores; at P are shown pollen grains two days after liberation from the mother cell wall, some of the grains being defective. × 450

restored. No opening takes place in an atmosphere more than about 85 per cent saturated. (Tables 2 and 3.)

TABLE 2.—*Data on dehiscence of ripe anthers when placed in moist and dry air at different temperatures*

Temperature	Humidity	Condition of anthers
3° C	Moist	Failed to dehisce.
	Dry	Dehisced in 5 days.
22° C	Moist	Failed to dehisce.
	Dry	Dehisced in 2 days.
23° C	Moist	Failed to dehisce.
	Dry	Dehisced in 18 hours.
32° C	Moist	Failed to dehisce.
	Dry	Dehisced in 6 hours.

TABLE 3.—*Summary of data or pollen dissemination at various times of day in 26 varieties of pecans in the Georgia Experiment Station orchard*

Date	6. p. m. to 6 a. m.				6 a. m. to 9 a. m.				9 a. m. to 12 m.				12 m. to 3 p. m.				3 p. m. to 6 p. m.			
	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter
1929	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*
Apr. 18																	66	68	1	39
Apr. 19	68	66	1	11	75	67	12	24	65	72	8	17	57	77	4	18	86	60	3	1
Apr. 20	60	86	3	32	65	74	6	24	61	77	11	54	61	77	7	71	51	70	10	10
Apr. 21	70	51	10	7	87	69	15	6	71	77	4	6	65	81	3	50	67	75	2	7
Apr. 22	75	67	2	4	70	72	14	31	65	74	15	84	69	72	11	69	78	65	3	74
Apr. 23	65	78	3	65	67	64	12	30	60	67	7	61	58	72	5	38	72	64	4	37
Apr. 24	64	72	4	63	81	64	4	27	70	72	6	128	66	77	7	248	76	70	1	129
Apr. 25	70	76	1	26	97	64	6	0	94	73	11	10	60	80	14	67	73	77	8	81
Apr. 26	77	63	8	5	81	62	9	18	76	64	8	0	75	63	8	0	80	59	4	28
Apr. 27	59	80	4	10	81	60	5	63	78	64	4	2	76	68	5	17	86	62	4	6
Apr. 28	62	86	4	13	83	72	12	0	81	74	13	37	90	72	8	13	98	61		0
Apr. 29	61	98		0	90	68	3	0	70	75	3	13	59	77	6	8	50	78	3	4
Apr. 30	78	50	3	10	74	63	7	16	83	70	2	24	83	80	4	10	90	64	4	1
May 1	64	90	4	0	90	72	6	0	81	77	9	2	83	76	7	16	81	70	3	0
May 2	70	81	3	0	78	74	11	4	90	67	12	9	77	58	12	1	90	49	10	0
May 3	49	90	10	0	72	55		0	69	62		2	68	62	10	1	75	58	2	0
May 4	58	75	2	0	75	62	5	0	65	70	7	1	86	62	2	2	65	64	4	0
May 5	64	65	4	0	60	77	6	1	75	73	9	1	75	75	4	1	78	72	3	6
May 6	72	78	3	0	85	73	8	0	82	76	9	1	71	80	9	5	69	79	3	2
May 7	79	69	3	0	90	72	9	0	87	75	10	2	84	73	11	4	87	69	10	5
May 8	69	86	3	2	80	68	10	17	72	74	3	4	93	64	6	0	93	64	2	0
May 9	64	93	2	0	95	62	8	0	90	66	6	0								
Average	66.6	76.2	3.9	11.9	79.8	67.3	8.4	12.4	75.5	71.4	7.9	21.8	72.8	72.3	7.2	32.0	76.7	66.6	4.2	20.2
1928																				
May 2					36	70	1	0	33	76	5	34	45	80	3	41	55	66	2	43
May 3	58	77	1	7	42	77	4	52	42	82	5	49	41	85	4	9	50	74	2	4
May 4	60	73	2	2	39	78	5	12	36	82	5	22	31	86	2	35	56	77	2	13
May 5	66	61	2	3	59	76	10	196	69	82	6	50	45	81	2	81	59	76	4	125
May 6	57	88	3	136	79	62	12	16												
May 7	49	86			85	52			93	50			93	49	9					
May 8													77	57	4	3	87	52	4	4
May 9	44	93	6	2	72	59	8	1	38	72	4	50	40	75	6	88	44	66	2	21
May 10	53	75	3	6	52	71	3	9	38	81	2	16	26	84	6	28	59	69	0	17
May 11	60	68	2	10	39	78	6	7	32	84	7	4	30	88	7	6	39	78	1	6

TABLE 3.—*Summary of data or pollen dissemination at various times of day in 26 varieties of pecans in the Georgia Experiment Station orchard*—Continued

Date	6 p. m. to 6 a. m.				6 a. m. to 9 a. m.				9 a. m. to 12 m.				12 m. to 3 p. m.				3 p. m. to 6 p. m.			
	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter
1928	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*
May 12	60	78	8	10	71	67	1	8	62	67	12	10	55	69	7	19	48	70	4	38
May 13	58	61	7	14	74	62	10	10	60	71	11	8	53	72	8	4	64	62	5	2
May 14	53	81	6	2	45	67	8	4	42	73	10	5	48	77	8	6	59	68	6	2
May 15	58	88	6	4	68	66	8	1	41	76	7	6	47	77	7	10	56	68	4	9
May 16	60	81	1	6	72	70	5	20	65	73	8	14	69	72	7	151	72	69	2	48
May 17	64	90	4	9	81	70	2	90	67	78	1	122	91	74	2	3	51	69	1	6
May 18	68	90	2	1	74	75	6	32	64	80	6	486	81	86	7	381	59	77	2	57
May 19	69	90	1	4	78	76	4	7	73	81	7	121	98	72	3	90	----	----	----	10
May 20	67	90	4	----	82	73	7	1	71	78	8	4	67	78	6	16	78	73	4	8
May 21	65	95	4	1	83	69	6	0	67	77	6	1	68	76	6	5	70	75	3	1
May 22	65	95	2	0	85	66	1	0	77	71	4	0	----	----	----	0	----	----	----	----
Average	59.7	82.1	3.6	12.8	65.8	69.2	5.6	24.5	56.3	75.5	6.3	55.7	58.2	75.6	5.5	51.4	59.2	69.9	2.5	23.0
1927																				
Apr. 22	----	----	----	----	----	----	----	6	----	----	----	7	----	----	----	3	----	----	----	6
Apr. 23	----	----	----	1	----	----	----	1	----	----	----	----	----	----	----	2	----	----	----	1
Apr. 24	----	----	----	0	----	----	----	0	----	----	----	1	----	----	----	2	----	----	----	5
Apr. 25	----	----	----	1	----	----	----	----	----	----	----	3	----	----	----	0	----	----	----	0
Apr. 26	----	----	----	0	----	----	----	1	----	----	----	0	----	----	----	1	----	----	----	4
Apr. 27	----	----	----	2	----	----	----	0	----	----	----	1	----	----	----	5	----	----	----	13
Apr. 28	----	----	----	6	----	----	----	3	----	----	----	2	----	----	----	18	----	----	----	55
Apr. 29	----	----	----	----	----	----	----	51	----	----	----	----	----	----	----	----	----	----	----	----
May 4	----	----	----	----	----	----	----	17	----	----	----	82	----	----	----	62	----	----	----	16
May 5	----	----	----	3	----	----	----	1	----	----	----	15	----	----	----	10	----	----	----	----
May 6	----	----	----	----	----	----	----	3	----	----	----	----	----	----	----	26	----	----	----	14
Apr. 7	----	----	----	19	----	----	----	12	----	----	----	1	----	----	----	----	----	----	----	----
Average	----	----	----	4	----	----	----	8.5	----	----	----	12.4	----	----	----	14.3	----	----	----	12.7

An idea of the maturity of pollen can be had from the stiffness of the catkin. A catkin that would not shed pollen within 48 hours is relatively stiff; one that would normally shed within 12 hours in warm, sunny weather is limber. Within two days after pollen is shed the catkin becomes dry, very stiff, and falls to the ground.

The stage of maturity of pollen can best be determined by the color of the anthers. From the time of emerging from the bud scales until 48 hours before pollen would normally shed under suitable conditions, the anthers are the same color as the bracts and leaves. After this time, however, the green color gradually disappears and the anthers take on more and more of the orange-yellow color of the pollen. When fully ripe the anther is pale greenish yellow. If conditions are suitable, dehiscence will occur immediately, but if the temperature is too low, or the humidity above about 85 per cent, the catkin may remain for five days or more without falling to the ground.

The rapidity of opening of ripe anthers depends somewhat on temperature but largely on the relative humidity of the air. On a warm, sunny day a single anther will completely shed its contents in an hour after opening begins. Due to variations in catkins, twigs, trees, and varieties under the same conditions, a single catkin will shed pollen for 2 days, a single tree will shed pollen for 5 or 6 days, a single variety will furnish pollen for 10 or 12 days, and a collection of three or more varieties of each group will furnish pollen for about 3 weeks.

If wilting was produced very rapidly by the high temperatures immediately after the catkins were removed from the tree, opening did not occur. Likewise, if the relative humidity was above 82 per cent the anthers remained closed. Partly or completely open anthers closed in a few minutes when subjected to a relative humidity of more than 90 per cent. Catkins that had fallen from the tree and become dry reabsorbed moisture and the anthers closed in the presence of high humidity.

Records taken in the orchard at 3-hour intervals showed that the time of most rapid shedding of pollen varied from day to day, depending on the temperature and the relative humidity of the air. No shedding occurred when the relative humidity was above 85 per cent. On some days the peak was reached before 9 a. m. On other days it was delayed until after 3 p. m., but it never occurred between 6 p. m. and 6 a. m. The temperature, relative humidity, and wind-velocity data in Table 3 were taken at the end of the time of exposure of the slides, and in some cases do not accurately indicate the conditions that prevailed during the period of exposure. The apparatus for catching pollen (fig. 1, A) remained in the same place throughout the pollen-shedding season for three years.

In 1928, in the midst of the pollen-shedding season, a period of 64 hours elapsed with no shedding because of rain. Three 24-hour periods occurred during the same season when no pollen was shed. As a result of low temperatures and high humidity in 1929, not more than 5 days out of 21 covered in the pollen-shedding season were really favorable for pollen dissemination. The relative humidity and temperature reached during clear nights with a gentle breeze were not sufficient to cause anthers already open to close, but they did prevent the further opening of anthers. A dew or rain which caused

the relative humidity to rise above 90 per cent caused all anthers to close and delayed shedding until several hours after sunrise on the following morning.

Since very high or very low temperatures do not occur at the time that pecans shed their pollen, the influence of temperature and wind velocity is chiefly indirect in regulating the relative humidity of the air. Though there is no opening of anthers during damp, rainy weather, immature anthers continue to reach the stage of maturity, therefore a period of high relative humidity followed by a prolonged period of low relative humidity is accompanied by the shedding of a very large quantity of pollen for several hours.

Close observation and careful records kept for a number of years (*30*) show that the length of the receptive period of the pistillate flowers is as responsive to conditions of temperature and humidity as that of staminate flowers. The same conditions which delay the shedding of pollen also prolong the receptive period of the stigmas. Trees on which the stigmas became receptive at a time unfavorable for pollen shedding and favorable for pollen germination did not have a heavy May "drop."

The effect of high humidity is mainly that of retardation. Instances have been observed in which stigmatic surfaces dried as much in 24 hours under dry, windy conditions as they did in two weeks of damp, cloudy weather. During a prolonged drought the susceptibility of the stigmatic surfaces to rapid drying increases as the receptive stage is approached, and on the second day after becoming receptive the roughened surface darkens, shrinks, and dies.

In rainy weather the receptive stage is reached very gradually, and after about 10 days the stigmatic surfaces show symptoms of drying. If cloudy weather continues the stigmas do not become completely dry for about 15 days. The normal period of receptivity of a single flower is about five days.

Observations of about 25 varieties for seven years show that during rainy seasons there are usually enough sunny days to effect pollination; and that dry weather, though optimum for pollen dissemination often precedes a heavy May drop. Data in this paper indicate that the degree of humidity optimum for pollen shedding is not sufficient to cause germination of pollen; also a low relative humidity markedly reduces the viability of the pollen.

Table 4 shows the amount of pollen caught on greased slides at various distances from pollen-shedding trees. The apparatus was always kept on the leeward side of the trees. The difference between the amount of pollen caught at a height of 10, 20, or 30 feet is insignificant. The amount of pollen that will be blown by the wind depends on the humidity, temperature, and velocity of the circulating air. The path of the pollen from a small group of trees is narrow at a given time, but the horizontal direction of air currents is likely to vary greatly during the 10 or 12 days of pollen shedding of a single variety. Throughout the southeastern part of the United States winds from the east and south are somewhat moist and are not as conducive to pollen shedding as winds from the west and northwest.

TABLE 4.—*Amount of pollen blown by a 2 to 5 mile-per-hour wind from a 20-year-old pecan orchard of Mobile, Stuart, and Teche varieties, 1927 and 1928*

Distance from orchard	Height from ground	Year and time of day	Pollen per square centimeter	Day after pollen shedding began
		1927		
	Feet		*Grains*	
500 feet	10	2 p. m. to 5 p. m.	70.7	First.
Do	20	do	80.7	Do.
Do	30	do	92.6	Do
Do	10	6 p. m. to 7 a. m.	0.8	Do.
Do	20	do	3.7	Do.
Do	30	do	4.5	Do.
800 feet	10	8 a. m. to 11 a. m.	137.8	Second.
Do	20	do	162.5	Do.
Do	30	do	156.5	Do.
Do	10	do	3.8	Fourth.
Do	20	do	5.2	Do.
Do	30	do	5.6	Do.
1,000 feet	10	11 a. m. to 2 p. m.	19.3	Do.
Do	20	do	28.0	Do.
Do	30	do	28.3	Do.
Do	10	2 p. m. to 5 p. m.	8.3	Do.
Do	20	do	16.6	Do.
Do	30	do	15.5	Do.
Do	10	5 p. m. to 7 a. m.	13.1	Do.
Do	20	do	21.4	Do.
Do	30	do	19.1	Do.
Do	10	7 a. m. to 11 a. m.	11.1	Fifth.
Do	20	do	13.2	Do.
Do	30	do	13.5	Do.
Do	10	11 a. m. to 2 p. m.	64.9	Do.
Do	20	do	107.1	Do.
Do	30	do	134.7	Do.
Do	10	2 p. m. to 5 p. m.	28.6	Do.
Do	20	do	44.8	Do.
Do	30	do	39.7	Do.
		1928		
3,000 feet	20	2 p. m. to 2 p. m.[a]	10.6	First.
Do	30	do	8.4	Second.
Do	10	do	10.6	Third.
Do	20	do	13.3	Fourth.
Do	30	do	13.6	Fifth.

[a] 24 hours.

TABLE 5.—*Dates on which pollen was shed and on which pistillate flowers were receptive of commercial varieties of pecans in leading pecan-growing centers of southeastern United States*

1926

Location and variety of pecan	Pollen shedding		Pistils receptive		Group	Self-pollinated
	Began	Ended	Began	Ended		
Tifton, Ga.:						
Alley	Apr. 27		Apr. 30		1	Yes.
Big Z	Apr. 29		Apr. 28		2	Yes.
Bradley	do		Apr. 26		2	Yes.
Curtis	Apr. 28		Apr. 28		2	Yes.
Delmas	May 1		Apr. 27		2	Yes.
Frotscher	May 4		Apr. 29		2	Yes.
Mobile	Apr. 26		Apr. 28		1	Yes.
Moneymaker	May 1		Apr. 27		2	Yes.
Moore	Apr. 26		Apr. 26		1	Yes.
Nelson	do		Apr. 27		1	Yes.
Pabst	do		Apr. 28		1	Yes.
President	Apr. 28		Apr. 30		2	Yes.
Schley	Apr. 29		Apr. 28		2	Yes.
Stuart	Apr. 30		Apr. 29		2	Yes.
Summers	Apr. 26		Apr. 28		1	Yes.
Teche	Apr. 30		do		2	Yes.
Van Deman	Apr. 28		Apr. 25		2	Yes.

TABLE 5.—*Dates on which pollen was shed and on which pistillate flowers were receptive of commercial varieties of pecans in leading pecan-growing centers of southeastern United States*—Continued

Location and variety of pecan	Pollen shedding		Pistils receptive		Group	Self-pollinated
	Began	Ended	Began	Ended		
1927						
Tifton, Ga.:						
Alley	Apr. 21		Apr. 29		1	No.
Big Z	Apr. 29		May 7		2	No.
Bradley	Apr. 21		Apr. 28		2	No.
Curtis	Apr. 22		May 3		2	No.
Delmas	Apr. 26		Apr. 29		2	Yes.
Frotscher	Apr. 12		Apr. 18		2	Yes.
Mobile	Apr. 29		May 6		1	No.
Moneymaker	Apr. 18		Apr. 21		2	Yes.
Moore	Apr. 21		Apr. 26		1	Yes.
Nelson	Apr. 9		Apr. 22		1	No.
Pabst	Apr. 18		Apr. 29		1	No.
President	Apr. 21		Apr. 26		2	Yes.
Schley	do		Apr. 29		2	No.
Success	do		do		1	No.
Teche	do		do		2	No.
Van Deman	Apr. 26		do		2	Yes.
1928						
Tifton, Ga.:						
Alley	Apr. 30		May 5		1	Yes.
Big Z	Apr. 28		May 7		2	No.
Bradley	do		May 5		2	No.
Mobile	Apr. 30		May 3		1	Yes.
Moneymaker	do		May 5		2	Yes.
Moore	Apr. 28		May 2		1	Yes.
Nelson	Apr. 21		Apr. 28		1	No.
Pabst	Apr. 30		May 2		1	Yes.
President	do		May 5		2	Yes.
Schley	Apr. 28		May 2		2	Yes.
Success	do		May 5		1	No.
Teche	Apr. 30		do		2	Yes.
1929						
Tifton, Ga.:						
Alley		Apr. 20	Apr. 22		1	No.
Big Z	Apr. 22			Apr. 20	2	No.
Bradley	do				2	No.
Curtis	Apr. 24			Apr. 21	2	No.
Delmas		Apr. 18		Apr. 20	2	Yes.
Frotscher	Apr. 23			Apr. 21	2	No.
Mobile		Apr. 19	Apr. 22		1	No.
Moneymaker	Apr. 21		Apr. 21		2	Yes.
Moore		Apr. 18	Apr. 20		1	No.
Nelson		Apr. 22	Apr. 25		1	No.
Pabst		Apr. 21	Apr. 24		1	No.
President	Apr. 20			Apr. 20	2	Yes.
Rome		Apr. 18	Apr. 22		1	No.
Schley	Apr. 21		Apr. 21		2	Yes.
Stuart	Apr. 24			Apr. 21	2	No.
Success		Apr. 18	Apr. 22		1	No.
Summers		Apr. 19	Apr. 21		1	No.
Teche	Apr. 23			Apr. 20	2	No.
Van Deman	do		Apr. 22		2	Yes.
Williams	do		Apr. 23		2	Yes.
Cordele, Ga.:						
Frotscher	Apr. 20		Apr. 20		2	Yes.
Mobile	Apr. 20			Apr. 29	1	No.
Moore	Apr. 18		Apr. 20		1	Yes.
Nelson		Apr. 18	Apr. 21		1	No.
Schley	Apr. 20		Apr. 20		2	Yes.
Stuart	do		do		2	Yes.
Van Deman	Apr. 23			Apr. 19	2	No.
Albany, Ga.:						
Schley	Apr. 22			Apr. 25	2	Yes.
Stuart	do			Apr. 26	2	Yes.
Van Deman	do			Apr. 25	2	Yes.

TABLE 5.—*Dates on which pollen was shed and on which pistillate flowers were receptive of commercial varieties of pecans in leading pecan-growing centers of southeastern United States*—Continued

1929

Location and variety of pecan	Pollen shedding		Pistils receptive		Group	Self-pollinated
	Began	Ended	Began	Ended		
Monticello, Fla.:						
Curtis	Apr. 21		Apr. 19	Apr. 25	2	Yes.
Frotscher	Apr. 24			Apr. 22	2	No.
Mahan	Apr. 21			Apr. 23	2	Yes.
Moore		Apr. 18	Apr. 21		1	No.
Russell	Apr. 20			Apr. 22	2	Yes.
Schley	Apr. 22		Apr. 22		2	Yes.
Stuart	Apr. 24		Apr. 23		2	Yes.
Teche	Apr. 22		Apr. 21		2	Yes.
Experiment, Ga.:						
Alley	Apr. 18	Apr. 24	Apr. 28	May 8	1	No.
Appomattox	Apr. 28	May 3	Apr. 22	May 1	2	Yes.
Beverage	Apr. 18	Apr. 24	do	May 6	1	Yes.
Bradley	Apr. 29	May 7	do	Apr. 26	2	No.
Centennial	Apr. 18	Apr. 25	Apr. 25	May 3	1	No.
Curtis	Apr. 30	May 12	Apr. 23	May 2	2	Yes.
Delmas	do	May 7	Apr. 21	do	2	Yes.
Indiana	May 6	May 12	Apr. 30	May 8	2	Yes.
Jerome	Apr. 21	Apr. 30	Apr. 24	May 9	1	Yes.
Mantura	Apr. 18	Apr. 23	Apr. 22	May 1	1	Yes.
Mobile	do	Apr. 24			1	No.
Moore	do	Apr. 23	Apr. 22	Apr. 30	1	Yes.
Nelson	do	Apr. 24	do	do	1	Yes.
Pabst	Apr. 20	do			1	No.
Randal	Apr. 18	Apr. 27				No.
Robson	do	Apr. 24	Apr. 23	May 3	1	Yes.
Rome	Apr. 20	Apr. 30	Apr. 24	May 9	1	Yes.
San Saba	Apr. 21	Apr. 26	do	May 8	1	Yes.
Schley	Apr. 29	May 7	Apr. 22	May 3	2	Yes.
Stuart	do	May 8	do	May 7	2	Yes.
Success	Apr. 22	Apr. 26	Apr. 25	May 9	1	Yes.
Teche	Apr. 29	May 7	Apr. 20	Apr. 24	2	No.
Van Deman	May 1	May 8	Apr. 21	Apr. 28	2	No.
Thomasville, Ga.:						
Frotscher	Apr. 22			Apr. 21	2	No.
Mobile		Apr. 18	Apr. 22		2	No.
Stuart	Apr. 22			Apr. 24	2	Yes.
Schley	do			do	2	Yes.
Athens, Ga.:						
Alley		May 3	May 6	May 13	1	No.
Delmas	May 6	May 15	May 3	May 11	2	Yes.
Frotscher	Apr. 31	May 6	May 1	May 9	2	Yes.
Jerome		do	May 5	May 13	1	Yes.
Mobile		do			1	No.
Nelson		May 3			1	No.
Pabst	May 1	May 9	May 6	May 13	1	Yes.
Success	May 7	May 13			1	Yes.
Schley	May 6	do	May 2	May 10	2	Yes.
Stuart	do	May 14	May 3	May 12	2	Yes.
Teche	May 7	do	May 2	May 11	2	Yes.
Van Deman	May 6	May 15	Apr. 30	May 9	2	Yes.
Raleigh, N. C.:						
Appomattox	May 3	do	Apr. 29	May 10	2	No.
Bradley	May 6	do		May 1	2	Yes.
Curtis	May 10	May 23	May 1	May 19	2	Yes.
Delmas	May 9	May 19	May 3	May 11	2	Yes.
Frotscher	May 7	May 21		May 3	2	No.
Georgia		May 6	May 5	May 23	1	Yes.
Krakezy		May 1	do	May 21	1	No.
Louisiana	May 6	May 15		May 8	2	Yes.
Manture		May 5	May 5	May 18	1	No.
Mobile		May 1	May 1	May 23	1	No.
Moneymaker	May 5	May 16		May 3	2	No.
Pabst	May 1	May 15	May 3	May 23	1	Yes.
President	May 10	May 23	May 1	May 11	2	Yes.
Russel	May 9	May 19	May 3	May 10	2	Yes.
Schley	May 10	May 23	May 1	May 17	2	Yes.
Sovereign		May 3	May 3	May 24	1	No.
Stuart	May 5	May 21	May 1	May 13	2	Yes.
Success	do	May 18	May 3	May 24	1	Yes.
Teche	May 7	May 22	May 1	May 15	2	Yes.
Van Deman	May 10	May 21	do	May 10	2	No.

Table 5 contains incomplete data on dates of beginning and ending of pollen shedding and beginning and ending of receptivity of stigmas of 142 varieties from eight pecan-producing sections in these States.

In varieties of Group 1 there were 31 instances of homogamy and 25 instances of complete dichogamy, all of the latter being protandrous. In varieties of Group 2 there were 57 instances of homogamy and 29 instances of dichogamy—11 instances of protandry and 18 instances of protogyny.

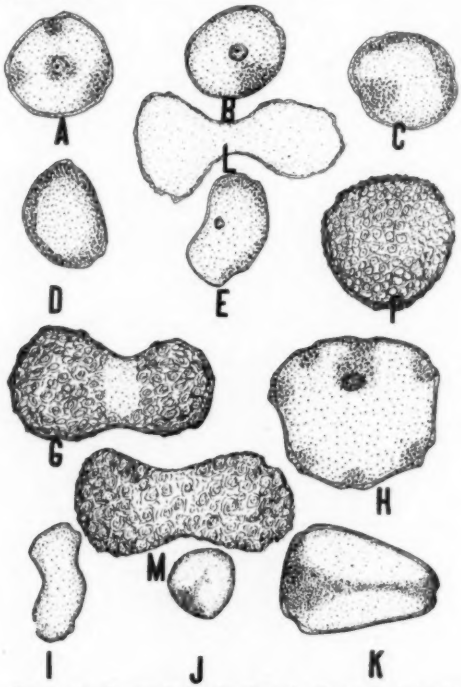

FIGURE 22.—Camera lucida drawings of pollen grains in lactic acid mounts: A, B, C, D, E, H, I, J, and K contain a small amount of finely granular cytoplasm; G and M are elongated grains; H, a grain with seven pores; F, a normal grain. × 850

EXAMINATION OF POLLEN

The writer has confirmed Stuckey's (*23*) observation that "in size, shape and general character, the pollen of the two groups of varieties of pecans differ almost none." However, the grains are not "rather flattened," as he described them.

Dry pollen grains from a single variety vary slightly in size and shape, are sculptured, and uniformly pale yellow. They are spherical but become shrunken immediately after shedding, and when exposed to very dry air the shrinking increases. Fresh pollen taken from an atmosphere 80 per cent saturated at 21° C. and placed in an oven at 32° lost 5.5 per cent moisture; when placed in an oven at 60° it lost 10 per cent. Dry grains containing no protoplasm can not be distinguished from those with protoplasm. Though the increased amount of shrinkage which accompanies the absence of protoplasm

may serve as a means of identifying certain defective grains, many abnormal grains appear normal when dry.

Normal pollen grains mounted in distilled water swell immediately and turn dark. Grains without protoplasm fail to swell, and grains containing protoplasm in less than the normal amount swell so that they are indistinguishable from normal grains.

When mounted in lactic acid, normal grains become light cream in color and spherical in outline, and assume in one minute an appearance distinct from defective grains. The latter either fail to swell and remain opaque, or swell and become almost transparent. The

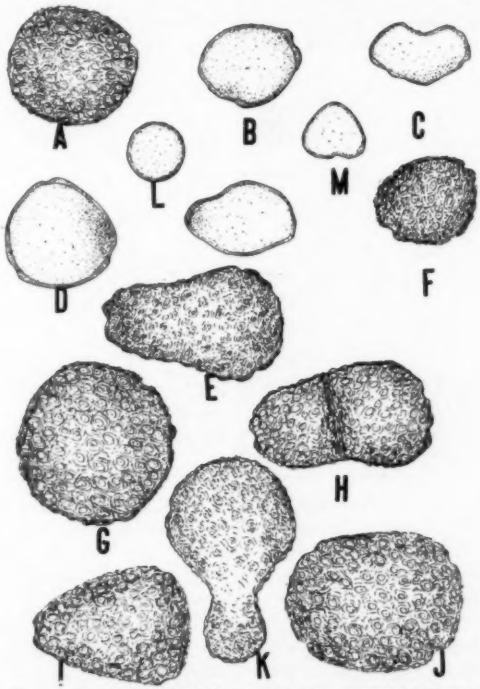

FIGURE 23.—Camera lucida drawings of pollen grains in lactic acid mounts: A, Normal grain with coarsely granular cytoplasm (Jerome); B, C, D, L, and M contain no cytoplasm (Jerome); F, a grain of less than normal size (Jerome); E, G, H (Jerome), I, K (Beverage), grains enlarged, abnormally shaped. × 800

lack of normal protoplasmic content in certain grains is clearly evident. Some grains are without either protoplasm or pores, indicating that abnormality began early in the development; others contain a small amount of protoplasm and one or more pores; still others have the normal number of pores and swell normally, but the protoplasm granules are very fine and sufficiently different from normal grains to be termed defective.

A single pollen grain observed in lactic acid amount is spherical with a roughened surface. When the percentage of normal grains is high they are extremely uniform in size, but if the percentage of

defective grains is high there are numerous large, small, and odd-shaped grains. (Figs. 22 and 23.) A normal grain is about 50 microns in diameter (*23*) with a wall about 2 microns in thickness. There is no appreciable difference in the size of pollen of any of the varieties studied except variations due to a large amount of defective pollen.

PERCENTAGE OF DEFECTIVE POLLEN

Table 6 contains data on the amount of defective pollen found when 169 lots were examined by the lactic acid method. The total number of grains examined was 169,000.

TABLE 6.—*Percentage of defective pollen as found by counting 1,000 grains in lactic acid mounts, 1928 and 1929* [a]

1928

Pecan variety and vigor	Average defective grains	Percentage of defective grains found at position indicated			Pecan variety and vigor	Average defective grains	Percentage of defective grains found at position indicated		
		Apex	Middle	Base			Apex	Middle	Base
Alley	19.5				Pabst:				
Atlanta	3.0	3.7	2.5	2.9	Vigorous	4.5	6.7	2.9	4.0
Beverage	6.7				Nonvigourous	4.4			
Bradley	8.3	10.2	8.9	6.3	Randal	5.9			
Centennial	35.1	33.5	34.5	37.1	Robson	7.1			
Curtis	6.3	8.6	6.7	4.1	Rome	29.6			
Delmas	5.4	4.4	7.6	4.1	San Saba:				
Frotscher	7.9	9.2	8.1	6.3	Vigorous	10.3	14.7	5.4	11.3
Indiana	6.4	6.0	7.3	6.0	Nonvigorous	13.4			
Jerome:					Schley	14.3	12.8	16.0	14.0
Vigorous	27.2	32.4	37.1	42.2	Stuart	46.6	81.7	27.6	20.6
Nonvigorous	35.2	31.6	33.5	40.5	Teche	7.5	8.0	5.1	9.4
Mantura	71.2				Unknown	13.1	12.2	9.4	17.6
Moneymaker	23.8	10.5	44.8	16.3	Van Deman	29.2	35.6	44.5	37.5
Moore	20.2				Wauchenah	5.8	5.7	6.3	5.3
Nelson	20.2								

1929

Pecan variety	Location	Vigor	Average defective grains	Percentage of defective grains found at position indicated		
				Apex	Middle	Base
Alley	Experiment, Ga.	Medium	10.2			
Appomattox	do	do	.3			
Beverage	do	do	.9	1.4	1.4	0
Bradley	do	do	6.9	7.7	4.4	8.5
Centennial	do	do	31.7			
Curtis	do	do	4.6			
Delmas	do	Vigorous	7.0			
Ga. Giant	Tifton, Ga.	do	10.4			
Indiana	Experiment, Ga.	Medium	3.3	4.3	2.3	4.4
Jerome	do	do	3.3			
Mahan	Monticello, Fla.	Vigorous	12.0			
Mantura	Experiment, Ga.	Medium	20.0			
McAlister	do	do	8.2			
Mobile	do	do	1.1	.8		1.4
Do	Cordele, Ga.	do	8.4			
Do	Milner, Ga.	Vigorous	1.7			
Do	Barnsville, Ga.	do	3.7			
Do	do	do	2.6			
Do	do	do	8.0			
Do	do	Medium	5.4			
Do	do	do	3.6			
Do	do	Not vigorous	3.0			
Do	do	do	2.3			

[a] Pollen from various pecan varieties when examined in 1929, 13 years after collection, showed the following percentages of defective grains: Frotscher, 4.5; Moneymaker, 6.2; Pan American, 9.8; President, 4.1; Teche, 30.6; Van Deman, 3.

TABLE 6.—*Percentage of defective pollen as found by counting 1,000 grains in lactic acid mounts, 1928 and 1929*—Continued

1929

Pecan variety	Location	Vigor	Average defective grains	Percentage of defective grains found at position indicated		
				Apex	Middle	Base
Moore	Experiment, Ga.	Medium	6.3	9.8	2.5	6.7
Nelson	do	do	5.6	5.4	4.6	6.8
Do	Barnsville, Ga.	do	12.3			
Pabst	Experiment, Ga.	do	1.0	1.1	.9	.9
President	Tifton, Ga.	do	6.5			
Robson	Experiment, Ga.	do	2.7	2.2		3.2
San Saba	do	do	5.2	2.9	3.7	7.8
Schley	do	do	5.9	6.5	5.6	5.7
Do	Baconton, Ga.	Vigorous	6.0			
Do	Griffin Ga.	Not vigorous	37.5			
Do	Tifton, Ga.	Vigorous	6.0			
Summers	do	do	16.4			
Stuart	Experiment, Ga.	do	7.2			
Success	do	do	3.7			
Teche	do	do	1.2			
Van Deman	do	do	41.0	36.6	46.0	41.5
Do	do	Not vigorous	32.1			
Do	Tifton, Ga.	Vigorous	40.0			
Do	Cordele, Ga.	do	9.6			
Do	Baconton, Ga.	Medium	26.0			
Wauchenah	Experiment, Ga.	Not vigorous	11.2			
Williams	Tifton, Ga.	Vigorous	10.4			
		Fertilizer				
Stuart	Experiment, Ga.	None	5.4			
Do	do	Complete	3.0			
Do	do	High P	5.6			
Do	do	High N	8.6			
Do	do	High K	7.2			
Do	do	Stable manure	6.5			

In 1928 pollen was much more plentiful in the orchards than in 1929, and the percentage of defective grains was about twice as high. The differences between the percentages of defective pollen shed from the apex, middle, and base of the same catkins is negligible. The Centennial and Mantura were the only varieties that produced pollen more than 19 per cent of which was defective in 1928 and 1929, and the Pabst was the only variety that produced pollen less than 5 per cent of which was defective in both years. The variation in percentages of defective pollen of the Mobile variety, taken from four localities and from trees of unequal vigor in 1929, is very small; also the variation in percentages of defective pollen taken from Stuart trees which received different kinds of fertilizers is insignificant. On the other hand, Schley pollen from nonvigorous trees at Griffin had about six times as high a percentage of defective pollen as that gathered at Experiment, Baconton, or Tifton, and Van Deman pollen from vigorous trees at Cordele had about one-third as high a percentage of defective pollen as that from trees of medium vigor at Baconton and about one-fourth as high as that from vigorous trees at Experiment or Tifton.

Table 7 shows the magnitude of variation of defective grains in successive lots of 100, that is, the percentage of defective grains in successive lots. The table includes 6 varieties and 12 lots of 1,000 grains each which were shown in Table 6. In general, it may be said that in counting 1,000 grains in lots of 100 grains each, the

lowest percentage of defective grains is about half that of the highest percentage.

TABLE 7.—*Magnitude of the variation (per cent) of defective grains as counted in successive lots of 100*

Percentage of defective grains at position mentioned in pollen from—									Percentage of defective grains in pollen from—		
Centennial			Jerome			Schley			Alley	Mantura	Curtis
Apex	Middle	Base	Apex	Middle	Base	Apex	Middle	Base			
34	32	30	33	33	44	11	20	13	30	57	54
30	34	32	19	35	38	13	14	21	16	72	51
35	30	33	36	47	42	9	16	15	16	80	52
35	34	44	24	37	40	15	15	12	13	57	53
32	38	41	40	33	45	10	22	9	17	74	54
33	40	44	30	35	43	16	17	8	19	74	77
43	29	42	36	46	47	10	13	16	25	68	60
34	36	34	31	34	54	15	17	13	21	77	56
45	34	33	40	39	39	17	14	18	17	28	56
19	38	38	35	30	30	12	12	14	21	81	48
33.5	34.5	37.1	32.4	37.1	42.2	12.8	16	14	19.5	71.2	56.1

The data recorded in Table 8 were obtained when the rubber-ring cells were used, as previously described.

TABLE 8.—*Pollen germination under varying conditions*

SERIES 1 [a]

Sugar used	Strength	Germination	Tube length	Grains bursting
	Per cent			
Maltose	20	0.5	Short	Few.
Do	15	.5	do	Do.
Do	10	1.0	do	Do.
Do	5	1.0	do	Do.
Sucrose	20	25.0	Long	None.
Do	15	30.0	do	Do.
Do	10	50.0	do	Do.
Do	5	40.0	do	Do.
Lactose	20	50.0	do	Do.
Do	15	40.0	do	Do.
Do	10	30.0	do	Do.
Do	5	30.0	do	Do.
Glucose	20	15.0	Short	Few.
Do	15	10.0	do	Do.
Do	10	5.0	do	Do.
Do	5	2.0	do	Do.
Fructose	20	0	do	Do.
Do	15	.5	do	Do.
Do	10	1.0	do	Do.
Do	5	1.0	do	Do.
Galactose	20	20.0	do	Do.
Do	15	15.0	do	Many.
Do	10	10.0	do	Do.
Do	5	5.0	do	Do.

[a] Using 2 per cent agar, pollen stored in laboratory for 24 hours, germination at 25° C., 4 drops of water in bottom of cell.

TABLE 8.—*Pollen germination under varying conditions*—Continued

SERIES 2[b]

Reagent added	Amount used	Germination	Tube length	Grains bursting	Remarks
	Per cent	*Per cent*		*Per cent*	
Asparagine	1.0	75	Long	10	
Do	.5	80	do	10	
Do	.1	85	do	10	
Tannic acid	1.0	0		0	
Do	.5	0		0	
Do	.1	0		0	
Peptone	1.0	20	Long	10	
Do	.5	50	do	15	
Do	.1	75	do	20	
Sodium hydroxide	1.0	0		0	Stained brown.
Do	.5	0		0	Do.
Do	.1	0		0	Do.
Do	.05	20	Long	20	
Do	.025	30	do	20	
Check		75	do	10	

SERIES 3[c]

Storage conditions	Storage period	Germination	Tube length	Grains bursting
	Hours	*Per cent*		
Fresh		70.0	Very long	None.
Laboratory	48	25.0	Medium	Do.
Desiccator	48	0		Do.
Moist chamber	48	30.0	Medium	Do.
25° C., dry	48	20.0	do	Do.
On ice	48	40.0	Short	Few.
Laboratory	72	15.0	do	Many.
Moist chamber	72	20.0	do	Do.
25° C., dry	72	0		None.
On ice	72	30.0	Short	Many.
Laboratory	96	.2	do	Few.
Moist chamber	96	10.0	do	Do.
On ice	96	20.0	do	Many.
Laboratory	120	0		None.
Moist chamber	120	5.0	Short	Do.
On ice	120	10.0	do	Many.
Moist chamber	144	0		None.
On ice	144	2.0	Short	Many.
In mail, moist	48	25.0	do	Do.
In mail, semimoist	48	20.0	do	Do.
In mail, dry	48	5.0	do	Do.
In mail, moist	192	5.0	do	Do.
In mail, semimoist	192	2.0	do	Do.
In mail, dry	192	0		Few.

[b] Using 10 per cent sucrose, 1½ per cent agar, Success pollen stored in laboratory for 24 hours, germination at 22° C., cell half filled with water.

[c] Using 20 per cent sucrose, 2 per cent agar, germination at 25° C., 4 drops of water in cell.

TABLE 8.—*Pollen germination under varying conditions*—Continued

SERIES 4 [4]

Pecan variety	Period of storage	Percentage germination under storage conditions indicated									
		32° C.		23° C.		22° C.		In orchard		5° C.	
		Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist
	Hours										
Schley	24	0	0	0	65	0	65	30	64	50	65
Stuart	24	0	0	0	80	0	80	45	80	65	80
Van Deman	24	0	0	0	50	0	50	25	45	45	50
Schley	48	0	0	0	50	0	55	0	60	25	60
Stuart	48	0	0	0	65	0	70	0	75	35	75
Van Deman	48	0	0	0	30	0	40	0	45	20	45
Schley	72	------	------	------	0	------	20	------	30	0	55
Stuart	72	------	------	------	.0	------	25	------	45	0	65
Van Deman	72	------	------	------	0	------	10	------	20	0	40
Schley	96	------	------	------	------	------	0	------	15	------	30
Stuart	96	------	------	------	------	------	0	------	25	------	40
Van Deman	96	------	------	------	------	------	0	------	10	------	25
Schley	120	------	------	------	------	------	------	------	0	------	3
Stuart	120	------	------	------	------	------	------	------	0	------	5
Van Deman	120	------	------	------	------	------	------	------	0	------	0
Beverage	120	0	0	0	0	0	0	0	0	0	0
Nelson	120	0	0	0	0	0	0	0	0	0	3
Robson	120	0	0	0	0	0	0	0	0	0	2
Centennial	120	0	0	0	0	0	0	0	0	0	0
Alley	120	0	0	0	0	0	0	0	0	0	1

SERIES 5 [4]

Germinating temperature	Percentage germination of—			Germinating temperature	Percentage germination of—		
	Schley	Stuart	Van Deman		Schley	Stuart	Van Deman
3° C	0	0	0	23° C	65	80	50
22° C	60	75	50	32° C	0	0	0

[4] Using 20 per cent sucrose, 1½ per cent agar, germination at 23° C., cells half filled with water (percentage germination).

[4] Using 10 per cent sucrose, 1½ per cent agar, cell half filled with water, fresh pollen.

Media containing 10 per cent sucrose, 1½ per cent agar, plus either one of the following formed a precipitate, failed to solidify at 20° C., and was not used: United States Pharmacopoeia citric acid, 1, 0.5, and 0.1 per cent; 91 per cent lactic acid, 0.5 and 0.1 per cent; United States Pharmacopoeia tannic acid, 1 per cent.

Under suitable conditions pollen began to germinate in 1½ hours and completed germination in 12 hours, but 14 to 18 hours were required for pollen tubes to reach full length before bursting. If allowed to remain longer than about 18 hours the tubes burst and emptied their contents into the surrounding medium. (Fig. 24.)

Bursting of pollen tubes is distinct from "pseudo germination" or bursting of ungerminated grains as described by Andronescu (*1*) and as used in Table 8. If the conditions remain favorable for growth all of the pollen tubes will burst in about 30 hours.

No tubes in artificial media have been found to branch, as occurs in the tube growth in the pistils (*31*); nor has any of the germination percentages equaled the percentage of normal pollen as shown by counts in lactic acid.

Pollen failed to germinate in pure water, or in any concentration of agar which did not solidify at 25° C. Satisfactory results were obtained with 1½ or 2 per cent agar when sugar was added. No germination was obtained when no water was placed in the cell to provide moisture for the pollen. From four to eight drops of water were found best for this; less than this amount did not keep the pollen sufficiently moist for germination, and much more than this caused excessive bursting of grains.

Data in Table 8 show that of the six sugars used in the media for germinating pollen, lactose and sucrose gave highest percentage

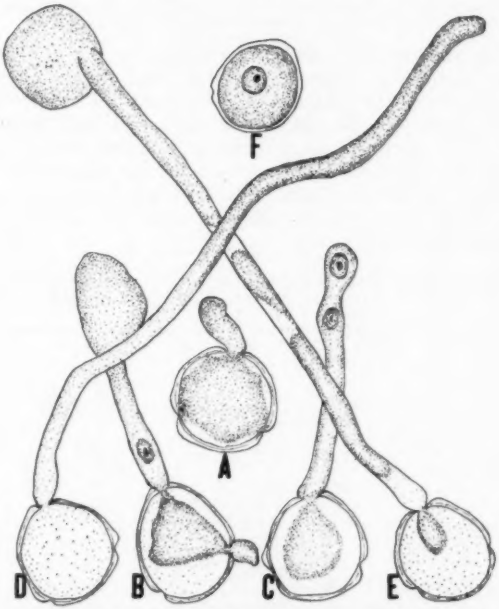

FIGURE 24.—Camera lucida drawing of stages in the germination of pollen grains on sugar-agar medium: A, Normal germination; B, formation of two tubes from a single pollen grain; B and E, swelling at end of tube which may later burst; C, two nuclei in the pollen tube; D, a normal tube; F, section of a pollen grain 10 days before shedding. × 750

germination and least bursting of the grains; galactose and glucose produced fair germination; and fructose and maltose caused an extremely low percentage germination and a high percentage of bursting.

One-tenth of 1 or one-half of 1 per cent asparagine when added to the medium produced a slight increase in percentage of germination; 1 per cent neither increased nor decreased the percentage of germination. More than 0.1 per cent of peptone caused a decrease in percentage of germination. Tannic acid prevented germination when 1, 0.5, or 0.1 per cent was added to the medium. Sodium hydroxide decreased germination when as low as 0.025 per cent was added to the medium, and more than 0.1 per cent prevented germination.

Pollen was stored under ten temperature and humidity conditions. That stored under both moist and dry atmospheric conditions at 32° C. lost its vitality in 24 hours. That stored at either 23° or 22° in a dry atmosphere did not germinate after 24 hours, but other lots germinated after being stored for 48 and 72 hours, respectively, under moist conditions. That stored dry at 5° germinated after 48 hours, and that stored moist germinated after 96 hours. No temperature and humidity condition was found under which pollen could be stored for longer than 96 hours with certainty of germination. The optimum temperature for germination was found to be about 23° C.

RELATION OF SIZE OF CROP PRODUCED IN ONE YEAR TO NUMBER OF FLOWERS PRODUCED THE FOLLOWING YEAR

In Table 9 is shown the relation between the size of crop of nuts of one year and the size of crop of staminate and pistillate flowers of the next year. In order that the data from trees of different varieties and ages might be comparable, each tree was rated and placed in one of six groups. The summary of all varieties shows that a large or very large crop of nuts is followed by a somewhat reduced crop of both staminate and pistillate flowers the following season; and no crop or a fair, poor, or very poor crop of nuts is followed by a large crop of both staminate and pistillate flowers.

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*

[A = very large crop; B = large crop; C = fair crop; D = poor crop; E = very poor crop; F = no crop]

Pecan variety	Age of tree	1928 crop of nuts	1928 crop rating	Rating of 1929 crop of—	
				Catkins	Pistillate flowers
	Years				
Alley	7	0.6 pound	D	C	B
Do	7	0.1 pound	D	C	B
Do	7	do	D	C	B
Do	18	34 pounds	C	A	D
Do	20	44 pounds	C	A	D
Appomattox	18	37 pounds	B	F	B
Atlanta	20	57 pounds	A	F	F
Beverage	20	21 pounds	D	A	A
Bradley	20	58 pounds	B	C	A
Centennial	20	3 pounds	E	B	C
Curtis	18	29 pounds	B	F	E
Delmas	12	10 pounds	D	A	A
Do	18		D	B	A
Do	18		D	B	A
Do	18		D	B	A
Do	20		E	A	A
Do	20		E	A	A
Do	20		E	A	A
Frotscher	20	110 pounds	A	F	F
Do	20	100 pounds	A	F	F
Do	16	3,259 nuts	A	E	A
Do	16	4,895 nuts	A	E	A
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Indiana	12	5 pounds	E	A	B
Do	12	6 pounds	E	A	B
Jerome	20	44 pounds	C	A	A
Mantura	20	34 pounds	C	A	F

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*—Continued

Pecan variety	Age of tree	1928 crop of nuts	1928 crop rating	Rating of 1929 crop of—	
				Catkins	Pistillate flowers
	Years				
Mobile	18	63 pounds	A	E	F
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18	3,202 nuts [a]	F	A	A
Do	18	2,938 nuts [a]	A	A	D
Do	18	4,704 nuts [a]	A	A	C
Do	18	856 nuts	D	A	A
Do	25	22,735 nuts [a]	A	F	F
Do	22	15 pounds	D	B	B
Do	11	41 pounds	A	F	F
Do	11	54 pounds	A	F	F
Do	11	28 pounds	A	F	F
Do	11	29 pounds	A	F	F
Do	11	25 pounds	A	F	F
Do	11	33 pounds	A	F	F
Do	11	43 pounds	A	F	F
Moneymaker	20	46 pounds	C	F	F
Moore	12	21 pounds	B	A	A
Do	12	6 pounds	E	A	A
Nelson	20	110 pounds [a]	A	B	F
Do	18	66 pounds [a]	A	B	F
Do	19		A	E	B
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	B
Do	16	1,504 nuts [a]	A	A	B
Do	16	1,354 nuts [a]	A	A	C
Do	16	1,779 nuts [a]	A	A	B
Pabst	20	91 pounds	A	B	F
Randal	20	96 pounds	A	F	F
Robson	20	48 pounds	C	B	D
Rome	12	11 pounds	C	B	B
Do	20	40 pounds	C	B	B
San Saba	18	25 pounds	C	B	B
Schley	12	55 pounds	A	E	E
Do	18		A	C	A
Do	18		A	C	A
Do	18		A	C	A
Do	8	17 pounds	B	C	C
Do	9	22 pounds	B	D	E
Do	18		A	C	A
Do	18		A	C	A
Do	18		A	B	A
Do	18		A	B	B
Do	18		A	B	B
Do	22		D	B	B
Do	22		D	B	B
Do	22		D	B	B
Do	22		D	C	B
Do	22		E	C	B
Do	16	615 nuts	B	D	B
Do	18	689 nuts	C	D	B
Stuart	20	2 pounds	E	A	B
Do	18	2,161 nuts	C	B	B
Do	18	1,961 nuts	C	B	B
Do	18	999 nuts	D	B	B
Do	18	2,136 nuts	C	B	B
Do	18	1,273 nuts	C	B	B
Do	18	992 nuts	D	B	B
Do	18	1,533 nuts	C	B	B
Do	16	852 nuts	C	C	B

[a] Nuts poorly filled.

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*—Continued

Pecan variety	Age of tree	1928 crop of nuts	1928 crop rating	Rating of 1929 crop of—	
				Catkins	Pistillate flowers
	Years				
Stuart	16	717 nuts	C	A	B
Do	16	1o4 nuts	D	A	A
Do	18	763 nuts	D	A	A
Do	18	607 nuts	D	A	A
Do	18	625 nuts	D	A	A
Do	18	663 nuts	D	B	A
Do	11	3 pounds	E	A	B
Do	11	2 pounds	E	A	B
Do	11	7 pounds	E	A	B
Do	11	1 pound	E	A	B
Do	11	4 pounds	E	A	B
Do	11	17 pounds	C	A	B
Do	11	1 pound	E	A	B
Do	11	4 pounds	E	A	B
Do	11	3 pounds	E	A	B
Do	11	7 pounds	E	A	B
Do	11	16 pounds	C	A	B
Do	11	3 pounds	E	A	B
Do	11	13 pounds	D	A	B
Do	11	9 pounds	D	A	B
Do	11	12 pounds	D	A	B
Do	11	17 pounds	C	A	B
Do	11	17 pounds	C	A	B
Do	11	6 pounds	E	A	B
Do	11	9 pounds	D	A	B
Do	11	1 pound	E	A	B
Do	11	16 pounds	C	A	B
Do	11	9 pounds	D	A	B
Do	11	9 pounds	D	A	B
Do	11	6 pounds	E	A	B
Do	11	6 pounds	E	A	B
Do	11	17 pounds	C	A	B
Do	11	6 pounds	E	A	B
Do	11	8 pounds	D	A	B
Do	11	11 pounds	D	A	B
Do	11	16 pounds	C	A	B
Do	11	8 pounds	D	A	B
Do	11	2 pounds	E	A	B
Success	12	4 pounds	E	A	A
Teche	20	55 pounds	B	D	D
Do	20	81 pounds	A	F	F
Do	20	61 pounds	B	D	F
Do	20	71 pounds	A	F	F
Do	18	288 nuts	E	B	A
Do	18	1,083 nuts	C	B	A
Do	18	1,167 nuts	C	C	A
Do	18	434 nuts	D	B	A
Do	11	24 pounds	B	F	C
Do	11	21 pounds	B	D	C
Do	11	18 pounds	B	E	C
Do	11	8 pounds	C	D	D
Do	11	18 pounds	B	E	F
Do	11	15 pounds	C	D	F
Do	11	7 pounds	B	B	F
Do	11	24 pounds	C	C	F
Do	11	20 pounds	A	A	F
Van Deman	20	19 pounds	C	A	F
Do	19		C	A	C
Do	19		C	A	C
Do	19		C	A	C
Do	19		C	A	C
Do	19		C	A	C
Do	19		E	A	A
Do	19		E	A	A
Wilson	12		C	A	C
Do	12		C	A	C

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*—Continued

Pecan variety	Age of tree	1926 crop rating	Rating of 1927 crop of—		Pecan variety	Age of tree	1926 crop rating	Rating of 1927 crop of—	
			Catkins	Pistillate flowers				Catkins	Pistillate flowers
	Years					*Years*			
Mobile	9	A	F	F	Stuart	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Stuart	9	C	A	A	Do	9	C	A	A
Do	9	C	A	A	Teche	9	C	A	F
Do	9	C	A	A	Do	9	C	A	B
Do	9	C	A	C	Do	9	C	A	B
Do	9	C	A	A	Do	9	C	A	F
Do	9	C	A	A	Do	9	C	A	B
Do	9	C	A	A	Do	9	C	A	B
Do	9	C	A	A	Do	9	C	A	C
Do	9	C	A	A	Do	9	C	A	C
Do	9	C	A	A	Do	9	C	A	C
Do	9	C	A	A	Do	9	C	A	F

SUMMARY OF ALL VARIETIES

Previous year's crop of nuts	Current year's crop of—											
	Catkins						Pistillate flowers					
	A	B	C	D	E	F	A	B	C	D	E	F
56 A's	5	6	7	0	14	24	10	7	1	1	2	35
27 B's	2	0	15	5	2	3	2	14	4	1	2	4
71 C's	52	13	2	3	0	1	24	23	11	5	0	8
31 D's	16	14	1	0	0	0	12	19	0	0	0	0
29 E's	26	2	1	0	0	0	9	19	1	0	0	0
6 F's	6	0	0	0	0	0	6	0	0	0	0	0

DISCUSSION

The general course of development of the pollen of the pecan is the same as that of other fruits. The fact that floral differentiation occurs a year before the pollen sheds shows that either the quantity or the quality of pollen may be influenced by the condition of the trees during the summer, fall, or winter previous to the shedding of pollen. On the other hand, pistillate flower differentiation occurs only about four months before the flowers become receptive. Therefore it would be expected that the condition of the tree during the previous year would influence staminate flower development much more than it would pistillate flower development.

Irregularities and abnormalities were found in the development of pollen in both groups of varieties. In a few cases there were rather high percentages of defective pollen. However, in view of the rather universal abundance of catkin formation, and therefore of pollen, it seems unlikely that pollen defects or impotence are factors of im-

portance in limiting the setting of fruit, except in cases of an isolated tree or variety, and then only when conditions are such as to cause a failure of staminate flowers to develop.

On the other hand, the more or less complete dichogamy that characterizes the pecan may occasion pollination difficulties. This is accentuated by the fact that pollen shedding is practically inhibited when the humidity remains above a certain point for any considerable period. It is still further accentuated by the fact that the period of receptivity of the stigmas is greatly reduced if the weather is very dry. In selecting varieties, therefore, the question of securing proper pollination should be considered. For practical purposes it seems that at least two varieties of each group should be included in a commercial planting. This would provide for at least one variety to shed pollen early in the season and at least one variety to shed late. It also seems that the number of trees of either of these two varieties could be reduced to one-twentieth of the total number of trees.

SUMMARY AND CONCLUSION

Catkin primordia are differentiated in lateral buds on new shoots throughout the growing season. In varieties of Group 1, anthers are differentiated in the fall of the year in which the catkin primordia are formed; in varieties of Group 2 anthers are differentiated early the following spring.

No abnormal behavior was observed in the development of catkin primordia, individual flower primordia, archesporial-cell stage or the mother-cell stage, but abnormalities occurred in all varieties studied during the reduction-division stage.

The smear method for counting the number of tetrads per anther, and the lactic acid method for determining the percentage of defective grains of pollen, have been successfully applied to pecan pollen studies. A method for quantitatively catching pollen from the air at various distances from pollen-shedding trees and at various heights from the ground was developed.

Though an entirely satisfactory method for germinating pecan pollen has not been developed, much was learned about the temperature, humidity, and nutritional requirements for germination on artificial media. The longevity of pollen was found to be about equal to or less than the period of receptivity of the stigmas, which indicates that there must be a continuous shedding of pollen throughout the period of receptivity of the stigmas.

When 1,000 grains from each of 169 lots of pollen were examined by the lactic acid method, the defective grains were found to range from 0 to 81.7 per cent. Pollen produced on trees of low vigor or on trees which bore very heavy crops of catkins had a slightly higher percentage of defective grains than pollen produced on trees of high vigor or on trees which had a light crop of catkins.

Records of blooming dates showed that either homogamy, protandry, or protogyny may occur in pecans.

It was found that pollen sheds only when the relative humidity of the air is below about 85 per cent and that practically all shedding occurs between 9 a. m. and sundown.

Conditions which were optimum for pollen shedding were destructive to the vitality of pollen. Optimum conditions for shedding of pollen are those which exist in the orchard on a warm, sunny day;

and optimum conditions for germination are found in an orchard on a warm, dewy night.

From the data contained herein it seems that all of the methods of studying pecans which involve hand pollination, used by the writer and others, have been somewhat at fault in that account was not taken of the fact that during times of low humidity there may be an enormous amount of pollen in the air even at great distances from pollen-shedding trees.

The size of the crop of nuts of one year was found to influence the size of crop of both staminate and pistillate flowers of the following year. A very heavy crop of nuts usually follows and is followed by a lighter crop. Certain varieties of pecan produce a medium-size crop of staminate flowers, pistillate flowers, and nuts each year.

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INHERITANCE OF ANTHOCYAN PIGMENTATION IN RICE[1]

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INTRODUCTION

The organs of the principal rice varieties commercially grown in the United States are uncolored (green) in the vegetative condition. There are other rice varieties, however, in which one or more of the vegetative organs are colored. The colors present in these organs usually are purples and reds of varying shades and intensity.

The colors in the vegetative organs of rice are due to the presence of anthocyan pigments, although other pigments may be present. The anthocyan pigments, which are soluble in the cell sap, often mask to a large extent the appearance of chlorophyll in the different organs. The inheritance of colors due to anthocyan pigments has been studied in maize, stock, snapdragon, rice, and other species, and it has been found to be in accordance with Mendel's laws.

The studies reported in this paper were undertaken to determine the mode of inheritance of anthocyan color in crosses between rice varieties having white kernels and normally green vegetative organs and those having kernels red when hulled and certain of the vegetative organs colored.

In this paper the word "green" denotes normal green color, except in the case of awns, which are normally straw-colored at maturity, while the word "colored" or the name of the color is used to denote the presence of anthocyan pigmentation.

TERMINOLOGY OF GLUMES AND THEIR PARTS[3]

In many papers discussing rice varieties, the terminology of the various glumes is confusing. The two small glumes at the base of the spikelet are referred to variously as outer glumes, lower glumes, empty glumes, sterile glumes, or glumes 1 and 2. The lemma and palea, which inclose the flower and subsequently the kernel, are called variously the inner glumes, upper glumes, floral glumes, and glumes 3 and 4. In conformity with accepted American usage, the first pair, or outer glumes, will be designated simply as glumes, and the two floral glumes as lemma and palea, respectively.

The short excurrent tips of the major fibrovascular bundles of the floral glumes, of which the lemma bears usually one but sometimes

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[3] The writer is indebted to C. R. Ball for assistance in working out a satisfactory terminology for these organs.

three, and the palea one, have been referred to by many writers on oriental rices as the "apiculus of the glumes."

In rice varieties having the vascular apiculi colored, the pigment frequently extends to the immediately adjacent or subtending parenchymatous tissue at the apex of the lemma and the palea. The phrases "glume tips" and "glume apexes" have been used by writers abroad to designate either or both of these tissues. In the present paper these combined tissues, "glume tips" and "glume apexes," are called lemma and palea apexes.

MATERIAL AND METHODS

The five rice varieties used as female parents were Niro Vialone, Butte (C. I.[4] 1564), Colusa (C. I. 1600), Eureka, and an unnamed variety (C. I. 5346). These are all of the Japanese type. Niro Vialone is an early maturing Italian variety. Many of its vegetative organs are purplish in color. Normally it is awnless, but occasionally a purplish mucro, or awnlet, varying in length from 1 to 2 mm., may be observed. The lemma and palea apexes, the (outer) glumes, the stigmas, the pulvini, the bases of the ligules, the auricles, the leaf sheaths, the leaf blades, the nodes, and the internodes are all purplish in color. Butte is a midseason awned variety with only the awns and the apiculi reddish in color. Colusa is an early maturing awnless variety normally without any colored organs. Eureka is an early maturing awnless variety which has no color except in the apiculi, which are red. The unnamed variety (C. I. 5346) is an early maturing, partly awned variety, without any anthocyan color.

The four varieties used as male parents were Caloro, Colusa, Italian Red, and Wataribune. Caloro is a midseason, partly awned variety. Normally about one-half of the spikelets on a panicle are awnless. All the organs, including the awns, are without anthocyan color. Wataribune is a late maturing, partly awned variety, without colored organs. The red variety used as the male parent in two crosses is locally known as Italian Red because it is supposed to have been introduced into California with seed rice which came directly or indirectly from Italy. Italian Red is an early maturing, partly awned variety, the seeds of which shatter quite readily. It has purple awns, purplish leaf margins and leaf sheaths, and reddish-purple ligules, auricles, and pulvini. The nodes are dark purple, and the internodes near the nodes show a tinge of purple. The glumes, lemma and palea apexes, and stigmas are purplish, and the hulled kernels are red.

The cross Niro Vialone × Caloro was made by the writer at the Biggs Rice Field Station in the fall of 1922; the crosses Butte × Colusa and Eureka × Caloro in the fall of 1923; and the crosses Colusa × Italian Red, C. I. 5346 × Italian Red, and Niro Vialone × Wataribune in the fall of 1924.

The hybrid seeds obtained were sown in paper pots, one seed in each pot. The pots were irrigated as frequently as necessary to maintain suitable moisture conditions for germination and growth. After the seedlings had emerged the bottoms of the pots were removed and the seedlings were transplanted to the nursery. The plants were spaced from 8 to 12 inches apart in rows 2 feet apart. The rice was

[4] C. I. refers to accession number of the Office of Cereal Crops and Diseases, formerly Office of Cereal Investigations.

irrigated at frequent intervals after transplanting until the land was continuously submerged.

The F_2 and F_3 progenies were grown from seeds sown in the field nursery. The plants were spaced from 6 to 12 inches apart in rows 2 feet apart.

ASSUMPTION OF A THREE-FACTOR HYPOTHESIS

In the study of the color characters reported in the cross Niro Vialone × Caloro it is assumed that the factor *C* must be present in order that anthocyan color may develop in any of the organs. When the factor *P* is present with *C* the color of certain organs is purple or purple striped, but when *P* is absent and *C* is present their color is red. It is also assumed that the factor *A* is necessary for the full expression of the purple color in certain organs.

The colors in the Niro Vialone variety, therefore, are assumed to be due to the interaction of the three dominant complementary factors *ACP*. The Caloro variety possesses no anthocyan pigments and is assigned the factorial composition *acp*. The F_1 hybrids, therefore, would have the factorial constitution *AaCcPp* and would be purple. The selfed F_1 plants would produce F_2 progeny falling into eight phenotypic classes, of the genotypes and in the ratios shown in Table 1. For convenience in discussing the inheritance of color the phenotypes are numbered from 1 to 8, inclusive. (Table 2.)

TABLE 1.—*Genotypic classes resulting in F_2 from the cross Niro Vialone (AACCPP) × Caloro (aaccpp)*

Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	Class 8
1 *AACCPP*	1 *AACCpp*	1 *AAccPP*	1 *aaCCPP*	1 *AAccpp*	1 *aaCCpp*	1 *aaccPP*	1 *aaccpp*
2 *AACCPp*	2 *AACcpp*	2 *AAccPp*	2 *aaCCPp*	2 *Aaccpp*	2 *aaCcpp*	2 *aaccPp*	
2 *AACcPP*	2 *AaCCpp*	2 *AaccPP*	2 *aaCcPP*				
2 *AaCCPP*	4 *AaCcpp*	4 *AaccPp*	4 *aaCcPp*				
4 *AACcPp*							
4 *AaCCPp*							
4 *AaCcPP*							
8 *AaCcPp*							
27 *ACP*	9 *ACp*	9 *AcP*	9 *aCP*	3 *Acp*	3 *aCp*	3 *acP*	1 *acp*

TABLE 2.—*Phenotypic classes present in the F_2 progeny from the cross Niro Vialone (AACCPP) × Caloro (aaccpp)*

Class	Phenotypes	Color of organs
1	*ACP*	All organs under consideration, purple.
2	*ACp*	Awns and lemma and palea apexes, red; other organs, green.
3	*AcP*	All organs green.
4	*aCP*	Leaves and leaf sheaths, purple striped; awns, lemma and palea apexes, internodes, glumes, and stigmas, purple; all other organs, green.
5	*Acp*	All organs green.
6	*aCp*	Awns and lemma and palea apexes, red; other organs, green.
7	*acP*	All organs green.
8	*acp*	Do.

The inheritance of the color in the cross Niro Vialone × Caloro, using the 3-factor hypothesis as a basis for analysis, with data from other crosses, is presented in the following pages.

The awns that were present on the F_1 plants were purplish in color. Most of the spikelets were awnless, however. The leaves,

leaf sheaths, apexes, internodes, glumes, stigmas, ligules, auricles, pulvini, and nodes were purplish in color, but of a lighter purple than those of the Niro Vialone parent. Purple color, therefore, was dominant to green in F_1.

Four separate linkage groups for color inheritance were obtained in F_2, namely: (1) Colored leaves and leaf sheaths; (2) colored awns and lemma and palea apexes; (3) colored internodes, glumes, and stigmas; and (4) colored nodes, ligules, auricles, and pulvini.

The theoretical ratios in F_2 for plants within each of the color-linkage groups and the phenotypic classes of which they are made up are as follows:

Color of leaves and leaf sheaths.—Ratio 27 purple, phenotypic class 1; 9 purple striped, phenotypic class 4; 28 green, phenotypic classes 2, 3, 5, 6, 7, and 8.

Color of awns and lemma and palea apexes.—Ratio 9 purple, phenotypic classes 1 and 4; 3 red, phenotypic classes 2 and 6; 4 green, phenotypic classes 3, 5, 7, and 8.

Color of internodes, glumes, and stigmas.—Ratio 9 purple, phenotypic classes 1 and 4; 7 green, phenotypic classes 2, 3, 5, 6, 7, and 8.

Color of nodes, ligules, auricles, and pulvini.—Ratio 27 purple, phenotypic class 1; 37 green, phenotypic classes 2 to 8.

COLOR OF LEAVES AND LEAF SHEATHS

The normal color of the leaves and leaf sheaths in most rice varieties of the Japanese type is some shade of green. In certain varieties, however, the green in the leaves and leaf sheaths is partially masked by soluble anthocyan pigments, which are red, purple, or purplish black. The color in the leaves ordinarily is most pronounced at the base and along the margins, whereas that in the leaf sheaths usually is most pronounced along the midribs.

IN NIRO VIALONE × CALORO

The inheritance of color in the leaves and leaf sheaths was studied in a cross between Niro Vialone, an Italian variety having purplish leaves and leaf sheaths, and Caloro, having green leaves and leaf sheaths.

In this cross the leaves and leaf sheaths of the F_1 hybrid were purple, of a somewhat lighter shade than those of the female parent.

F_2 PROGENY

The segregation in F_2 for color of leaves and leaf sheaths is shown in Table 3. The data do not agree well with the expected 27:9:28 ratio. The probability that the deviations observed in this ratio are due to random sampling is only about 1 in 80, which indicates that some disturbing forces may be affecting the results in this case. These disturbing forces may be a fourth factor.

TABLE 3.—*Segregation of 207 F_2 hybrids from the cross Niro Vialone × Caloro for color of leaves and leaf sheaths, at Biggs, Calif., 1924*

Color of leaves and leaf sheaths	Number of plants—		Deviation
	Observed	Expected in 27:9:28 ratio [a]	
Purple	100	87.33	+12.67
Purple striped	15	29.11	−14.11
Green	92	90.56	+1.44

[a] $\chi^2=8.7004$. $P=0.0133$.

The plants with purple-striped leaves and leaf sheaths had green nodes, ligules, auricles, and pulvini, while in the purple-leaved group these organs were purple. The two groups, therefore, were very easily classified. The F_2 population was small; but, with a much larger population in the F_3 generation, the deviations from the expected 27:9:28 ratio are large, and the value for P shows a very poor fit. (See Table 5.)

If, on the assumption of a 3-factor hypothesis, the F_2 population is placed in four phenotypic groups, the data shown in Table 4 are obtained.

TABLE 4.—*Classification in four phenotypic groups of the F_2 population of the cross Niro Vialone × Caloro on the basis of a 3-factor hypothesis*

Phenotypes	Ratio	Observed	Calculated	$\frac{(o-c)^2}{c}$
All organs purple	27	100	87.33	1.8382
Leaves and leaf sheaths purple striped	9	15	29.11	6.8393
Awns and lemma and palea apexes red	12	30	38.81	2.0000
All organs green	16	62	51.75	2.0301
	64	207	207.00	$x=12.7076$

The value for P in this case is 0.0054, which indicates a poor fit. An inspection of the values of $\frac{(o-c)^2}{c}$ show that the second phenotypic group, plants having purple-striped leaves and leaf sheaths, are materially at variance, whereas the other groups do not vary markedly from the observed ratio. This indicates that the unknown disturbing forces are probably located in the purple-striped group.

The purple-striped group (*aCP*) differs from the purple group (*ACP*) for the factor *A*. By grouping the F_2 plants on the theoretical genotypic basis, the *C* factor is present in 145 colored plants and absent in 62 green plants.

These numbers agree well with a 3:1 ratio. The deviation is 10.25 plants with a probable error of ±4.20. The *C* factor appears, therefore, to segregate independently. The *P* factor is present in 161 F_2 plants and absent in 46. These numbers also agree with a 3:1 ratio. The deviation is 5.75 plants with a probable error of ±4.20. The *P* factor appears to segregate independently. The *A* factor is present in 100 F_2 plants and absent in 15 plants having purple-striped leaves and leaf sheaths. These numbers do not agree well with a 3:1 ratio. The deviation is 13.75 plants with a probable error of ±3.13. The deviation is more than four times the probable error, which indicates that some disturbing forces are affecting the results in this case. These forces may be a fourth factor. However, the segregations in F_2 and F_3 for all characters studied are in general agreement with the 3-factor hypothesis, except for the color of leaves and leaf sheaths.

Takezaki (*16*)[5] found that purple leaves were dominant to green in F_1 rice hybrids, and that segregation in F_2 was in the ratio of 27 plants with purple leaves to 37 with green. The correctness of this

[5] Reference is made by number (italic) to "Literature cited," p. 1127.

ratio was verified by growing F_3 progeny. This ratio indicates that, for the varieties used, the purple color was due to the interaction of three dominant genetic factors.

Hector (*2*, *3*), in studies on the inheritance of color in the leaf sheaths of rice, found that color was dominant to lack of color in F_1. In F_2 he obtained ratios of 3:1, 9:7, 15:1, and 27:37 for plants with colored and green leaf sheaths, respectively. Parnell and others (*13*), Roy (*15*), and Nagai (*12*) found that segregation in F_2 was in the ratio of 3 plants with colored leaf sheaths to 1 with green. The colored variety used by Roy (*15*) had striped leaf sheaths. Roy also reports one segregation that produced 9 plants with colored leaf sheaths to 7 with green. These results indicate that in some varieties of rice a single genetic factor is responsible for the color of the leaf sheaths, while in other varieties the development of color apparently is due to the interaction of two or three dominant complementary factors.

The deficiency in the purple-striped group is large but probably not large enough to warrant a rejection of the 3-factor hypothesis. It is possible that the seeds of the purple-striped plants do not germinate so well as those of the other two groups, or, if they do germinate as well, the seedlings may not be so hardy as those of plants with purple leaves. The death of the less hardy purple-striped seedlings would result in a deficiency in this group. There is no evidence that this has occurred here, but other experiments at Biggs have shown that under field conditions only one-half to two-thirds of the seeds sown produce seedlings, and many of these fail to reach maturity. Therefore, if there are differences in the hardiness of these three groups of plants, these differences could lead to a deficiency in one group and an apparent excess of plants in either or both of the other groups.

F_3 Progeny

To check the results obtained with the F_2 progeny and the 3-factor hypothesis indicated by them, F_3 populations were grown in 1925.

In all, 47 F_3 families were grown, 18 of which were from the purple group (phenotypic class 1), 9 from the purple-striped group (phenotypic class 4), and 20 from the green group (phenotypic classes 2, 3, 5, 6, 7, and 8). The 20 F_3 families from the green plants, consisting of 2,153 plants, all bred true for green leaves and leaf sheaths as was expected. The segregation of the F_3 progenies is shown in Table 5. Of the 18 F_3 families from the group having purple leaves and leaf sheaths, 4 families, consisting of 483 plants, bred true for purple leaves and leaf sheaths; 1 family segregated in the ratio of approximately 3 plants with purple leaves and leaf sheaths to 1 with these organs green; 1 family segregated in the ratio of 9 plants with purple leaves and leaf sheaths to 7 with green; and the remaining 12 families segregated into three groups similar to those obtained in F_2.

The large plus deviation for the purple group and the marked minus deviations for the purple-striped and green groups are the outstanding inconsistencies noted in Table 5. These large deviations no doubt are significant. Whether they are due, as has been suggested, to a fourth factor or a difference in the germination of the seed of each group or to a difference in hardiness which results in a higher mortality of the purple-striped and green seedlings has not been determined. The results do show, however, that some factor or factors, genetic or external, affected the results in this case.

TABLE 5.—*Segregation of F_2 progenies from the cross Niro Vialone × Caloro for color of leaves and leaf sheaths, at Biggs, Calif., 1925*

Color group of F_2 progeny and number of families	F_2 progenies having leaves and leaf sheaths—			Deviation from 3:1 ratio, and probable error	Deviation from 9:7 ratio, and probable error [a]
	Purple	Purple striped	Green		
Purple leaves and leaf sheaths:					
4	483				
1	93		21	−7.50±3.12	
1	70		58		−2.00±3.79
12	707	99	464		
Expected in a 27:9:28 ratio [b]	535.78	178.59	555.63		
Deviation	+171.22	−79.59	−91.63		
Purple-striped leaves and leaf sheaths:					
6		486	154	−6.00±7.39	
3		182	143		+0.81±6.03
Green leaves and leaf sheaths, and green leaves and leaf sheaths with red apexes:					
20			2,153		

[a] Probable errors for number of individuals where only two classes were concerned (see also Tables 7, 8, 12, and 13 and in text) were obtained from tables of probable errors of Mendelian ratios, calculated from the formula $\pm 0.6745\sqrt{pqn}$, prepared in the Department of Plant Breeding, Cornell University, Ithaca, N. Y.
[b] $\chi^2 = 105.2978$. P = very poor fit.

In none of the segregating F_3 purple families was there produced a ratio of 3 plants with purple leaves and leaf sheaths to 1 purple striped. This probably is due to the fact that an insufficient number of F_3 purple families was grown to include plants of all genetic constitutions. One can hardly expect to get true-breeding families and families that segregate in all four expected ratios from so small a number as 18 families.

Of the nine F_3 families from the purple-striped group, six segregated in the ratio of 3 plants with purple-striped leaves and leaf sheaths to 1 with green, and the remaining three segregated in a ratio of 9 plants with purple-striped leaves and leaf sheaths to 7 with green. Segregation in these ratios was expected, and also true-breeding plants with purple-striped leaves and leaf sheaths. The true-breeding form, however, was not obtained in F_3, but true-breeding plants with purple-striped leaves and leaf sheaths were selected from two of the families in 1925 and were grown in F_4 in 1926. The F_3 results from this group, therefore, are in agreement with expectations.

The data presented regarding the inheritance of color in the leaves and leaf sheaths of the F_1, F_2, and F_3 generations from the cross Niro Vialone × Caloro tend to support the 3-factor hypothesis, but they do not entirely confirm it. While all except one of the expected ratios were obtained in F_3 from the purple and purple-striped F_2 groups, the deviations from the calculated 27:9:28 ratio were large and no doubt significant. Additional support for the 3-factor hypothesis is found, however, in the results from the study of the color inheritance in other organs discussed later in this paper.

COLOR OF AWNS

The color of awns in rice varieties may be either green (straw colored at maturity), yellow, brown, red, purple, or black. Hector (*2*) and Ikeno (*5*) found in crosses of rice varieties with colored awns and with green awns that color was dominant in the F_1 hybrids, and

that in F_2 progenies segregation was in the ratio of 3 plants with colored awns to 1 with green. Koch (*9*, *10*) reported that black-awned and pink-awned forms appeared in the progeny from a cross of a white-awned and an awnless variety. In this case the colored awns no doubt were due to the action of complementary factors, one of which may have entered the cross from each variety. Nagai (*12*) found that in a cross of a brown-awned variety and one with pale yellow awns the awn color in F_1 hybrids was red, and segregation in F_2 was in the ratio of 9 red to 3 brown to 4 pale yellow. Hoshino (*4*) observed that black awns were dominant to green in F_1, but he did not report on the segregation for the color of awns in F_2.

IN NIRO VIALONE × CALORO

In the cross Niro Vialone × Caloro, in which Niro Vialone normally is awnless with purple lemma and palea apexes, and Caloro has green awns, the F_1 hybrid had a few purplish awns. Although Niro Vialone is normally awnless, it does under certain conditions produce a few short awns. Of the 207 F_2 plants grown, 181 had awns sufficiently developed to study their color. Of the F_3 families grown, one failed to produce awns that were long enough to be included in the study of color.

F_2 Progeny

In the F_2 progeny the segregation for awn color produced plants in the ratio of 9 purple to 3 red to 4 green, as is shown in Table 6. It is seen in Table 6 that there were 100 plants with purple awns, 25 with red, and 56 with green. The deviations from the expected numbers are small for each group.

TABLE 6.—*Segregation of 181 F_2 hybrids from the cross Niro Vialone × Caloro for color of awns, at Biggs, Calif., 1924*

Color of awns	Number of plants—		Deviation
	Observed	Expected in 9:3:4 ratio *	
Purple	100	101.81	−1.81
Red	25	33.94	−8.94
Green	56	45.25	+10.75

* $\chi^2=49.409$. $P=0.0852$.

It was observed that the purple awns often were red and sometimes parti-colored (red and green) upon emergence from the leaf sheaths, but rapidly changed to purple, and that the red awns may lose almost all of the red color by the time the panicles are fully matured. Errors in classification of the red-awned and green-awned groups, therefore, are possible late in the season.

F_3 Progeny

The purple-awned group consists of the phenotypic classes 1 and 4, the red-awned group of phenotypic classes 2 and 6, and the green-awned group of phenotypic classes 3, 5, 7, and 8. The data on F_3 families in all these groups are shown in Table 7.

From the purple-awned group (class 1) some families in F_3 should breed true for purple awns, and others should segregate in the ratios of 3 purple-awned plants to 1 red-awned plant, 3 purple-awned to 1 green-awned, and 9 purple-awned to 3 red-awned to 4 green-awned. True-breeding families and families segregating approximately in the stated ratios were obtained, as shown in Table 7.

TABLE 7.—*Segregation of F_3 progenies from the cross Niro Vialone × Caloro for color of awns, at Biggs, Calif., 1925*

Color group of F_2 progeny and number of families	F_3 progenies having awns—			Deviation from 3:1 ratio, and probable error
	Purple	Red	Green	
Purple leaves, leaf sheaths, and awns:				
2	73			
3	210		51	−14.25±4.71
3	63	21		0.00±2.68
6	166	64	109	
Expected in a 9:3:4 ratio [a]	190.69	63.56	84.75	
Deviation	−24.69	+0.44	+24.25	
Purple-striped leaves and leaf sheaths, and purple awns:				
5	266	85		−2.75±5.47
4	182	42	70	
Expected in a 9:3:4 ratio [b]	165.38	55.12	73.50	
Deviation	+16.62	−13.12	−3.50	
Green leaves, leaf sheaths, and awns:				
14			712	
Green leaves and leaf sheaths, with red awns and lemma and palea apexes:				
3		142		
2		62	29	+6.25±2.79

[a] $\chi^2=10.1386$. $P=0.0064$.

[b] $\chi^2=4.9598$. $P=0.0842$.

The expected and observed numbers for the 3:1 ratio are in good agreement. The deviations for the purple-awned and green-awned groups in the 9:3:4 ratio, however, are large, but they probably are not significant and may be due to seedling mortality or possibly to errors in classification.

The purple-striped group (class 4) should segregate for awn color in F_3 in the same manner as the purple group (class 1). The ratios obtained are shown in Table 7. The expected true-breeding purple-awned progeny and the ratio of 3 purple-awned plants to 1 green-awned plant were not obtained in F_3. This very likely is due to the fact that not enough F_3 families were grown to include plants of all genetic compositions. In F_4 true-breeding purple-striped progenies were observed, which indicates that if more F_3 families had been grown the true-breeding type would have been obtained. The expected and observed numbers for the 3:1 and 9:3:4 ratios obtained from the purple-striped group (class 4) are in good agreement.

The F_3 families from the red-awned group (classes 2 and 6) should produce true-breeding red-awned progeny, and also families that segregate in the ratio of 3 red-awned plants to 1 green-awned plant. Of the six F_3 families grown, 3 bred true for red awns, two segregated in the ratio of 3 red-awned plants to 1 green-awned plant, and one family bred true for awnless plants with red lemma and palea apexes. (Table 7.) The results in F_3 for the red-awned group therefore were in accordance with the expectation.

The F_3 families from the green-awned F_2 group (classes 3, 5, 7, and 8) should all breed true for green awns, and all 14 families grown did so.

The purple-awned, red-awned, and green-awned groups obtained in F_2, with two exceptions, therefore, produced the ratios and the true-breeding types expected in F_3 progenies. The exceptions noted probably are due to the fact that in all groups only a limited number of F_3 progenies was grown, and no doubt all genetic types were not included. This would account for the fact that two expected segregations were not obtained in F_3. Otherwise the results in F_3 are in fairly good agreement with the expected behavior and tend to confirm the 3-factor hypothesis, and the 2-factor difference for color of awns.

IN BUTTE × COLUSA

The Butte variety has red awns. Colusa is entirely awnless. In the cross Butte × Colusa the F_1 plants had red apiculi and red awns.

F_2 Progeny

The F_2 plants grown in 1925 segregated for awnedness and color of awns. In another study of this cross by the writer (*7*), 52 awnless and 785 awned and partly awned plants were reported. In this group with awns more or less developed there were 600 plants with red awns to 185 with green awns. The deviation from the expected numbers in a 3:1 ratio was 11.25 plants with a probable error of ±8.18. The segregation was in very close agreement, therefore, with the monohybrid 3:1 ratio.

F_3 Progeny

There were 16 F_2 plants which bred true for green awns in F_3. Seven of these F_3 families, however, segregated for awnedness, producing some awnless plants. Seven F_2 plants bred true for red awns, and four of these F_3 families segregated for awnedness, producing some awnless plants. Ten F_2 plants with red awns segregated for color of awns in F_3. There were 301 plants with red awns and 108 with green. The deviation from the expected numbers in a 3:1 ratio was not large for any of the F_3 families. The total number for all families agrees very well with the expected 3:1 ratio. The deviation from the expected ratio is 5.75 plants, and this deviation divided by the probable error, ±5.91, is less than unity. The results, therefore, indicate that one genetic factor is involved in the production of awn color in this case. In relation to awn color Butte apparently has the factorial constitution *Cp* and Colusa *cp*.

IN COLUSA × ITALIAN RED

The Colusa variety is awnless under all conditions and the apiculi are green. Italian Red rice is partly awned, and the awns range in color from purple to almost black. The partly awned F_1 plants from the cross Colusa × Italian Red had purple awns and lemma and palea apexes. Segregation in the F_2 population produced three groups of plants with respect to awn color. Their frequencies are indicated in Table 8.

The awns of F_2 plants often are parti-colored (red and green) when they first emerge from the sheaths, but within a relatively short time such awns either become red or deepen in color from red to purple.

The data on awn color from the cross Colusa × Italian Red presented in Table 8 agree very well with the numbers expected in a 9:3:4 ratio. The green group shows the largest deviation from the expected ratio. In this cross, color in the awns, therefore, is apparently due to the independent action of two genetic factors.

TABLE 8.—*Segregation of F_2 hybrids from the crosses Colusa × Italian Red and C. I. 5346 × Italian Red, and from both crosses for color of awns, at Biggs, Calif., 1926*

Cross and color group	Number of plants—		Deviation	χ^2	P
	Observed	Expected in a 9:3:4 ratio			
Colusa×Italian Red:					
Purple	198	203.0625	−5.0625	2.3167	0.3220
Red	61	67.6875	−6.6875		
Green	102	90.2500	+11.7500		
C. I. 5346×Italian Red:					
Purple	258	287.4375	−29.4375	6.8418	.0333
Red	109	95.8125	+13.1875		
Green	144	127.7500	+16.2500		
Total from both crosses:					
Purple	456	490.5	−34.5	6.2813	.0443
Red	170	163.5	+6.5		
Green	246	218.0	+28.0		

IN C. I. 5346 × ITALIAN RED

In the cross C. I. 5346 × Italian Red the F_1 plants had purple awns, and segregation of F_2 progeny produced three groups of plants with respect to awn color, as shown in Table 8.

Table 8 shows that there is a rather large minus deviation from the expected numbers in the purple group and fairly large plus deviations in the red and green groups. The explanation given below for the deficiency and excess of color in the lemma and palea apexes in the same cross also applies in this case. In each of these cases the deviation from the expected numbers in the 9:3:4 ratio is not exceedingly large, and the data indicate that in all probability the varieties used in this study of awn color differ by two independently inherited genetic factors.

Table 8 shows the combined data from the segregation in F_2 progeny for color of awns in the two crosses last discussed. It is observed that the deviations from the expected numbers in a 9:3:4 ratio are rather large for the purple and green groups. It is the opinion of the writer, however, that these deviations probably are due to errors in classification of F_2 plants and that the results can be explained on the basis of a 2-factor difference for awn color.

The data presented on the inheritance of awn color indicate that Italian Red has the factorial constitution *CP*, and Colusa and C. I. 5346, *cp*.

COLOR OF APICULI AND OF LEMMA AND PALEA APEXES

As previously noted, the term "apiculi" refers to the excurrent ends of fibrovascular bundles of the lemma and palea, whereas the term "lemma and palea apexes" includes not only the apiculi but also the immediately adjacent portion of these organs.

The color of the lemma and palea apexes is a character often used in classifying rice varieties. The apexes of the lemma and palea of Japanese rices most commonly are green or straw colored at maturity, but they may be brown, red, purple, or purplish black. Most rice varieties grown in the United States have green lemma and palea apexes, which become straw colored at maturity.

Hector (*2, 3*) found in crosses between a variety with colored apiculi and one with green that in the F_1 hybrids they were colored, and segregation in F_2 resulted in ratios of 3:1, 9:7, 15:1, and 27:37 plants with colored and green apiculi, respectively. Ikeno (*5*) and Parnell and others (*13*) found color in the apiculi dominant in F_1, and segregation in F_2 produced 3 colored plants to 1 green plant. These results indicate that colored apiculi may be due to a single-factor difference or to two or three dominant complementary factors or to dominant duplicate factors.

IN NIRO VIALONE × CALORO

The Italian variety Niro Vialone has purple or purplish lemma and palea apexes, whereas those of Caloro are green. In the F_1 hybrid from the cross Niro Vialone × Caloro the lemma and palea apexes were purple.

F_2 Progeny

Segregation in F_2 produced plants in the ratios of 9 with purple apexes to 3 with red to 4 with green. The number of plants in each group is shown in Table 9. The deviations from the expected numbers for each group are small.

As the color of the lemma and palea apexes and awns in the cross Niro Vialone × Caloro apparently is due to the same factors, and as the purple, red, and green groups for apexes are composed of the same phenotypic classes as those for awn color, it seems unnecessary to report here the detailed results obtained in F_3 on the inheritance of color of the lemma and palea apexes. The two expected ratios which were not obtained for awn color were not obtained for apex color. The possible reasons for this are the same as those discussed in the case of awn color. The differences in total number of plants reported in the study of awns and apexes in F_3 are due to the fact that some families were awnless but segregated for color of apexes.

TABLE 9.—*Segregation of 207 F_2 hybrids from the cross Niro Vialone × Caloro for color of lemma and palea apexes, at Biggs, Calif., 1924*

Color of apexes	Number of plants[a]		Deviation
	Observed	Expected in 9:3:4 ratio	
Purple	115	116.44	−1.44
Red	30	38.81	−8.81
Green	62	51.75	+10.25

[a] χ^2=4.0479. P=0.1328.

F_3 Progeny

In the F_3 progeny 4 F_2 plants having purple apexes, 14 having green apexes, and 3 having red apexes bred true. All expected ratios and true-breeding forms in F_3 were obtained, as is shown in

Table 10. The expected and observed numbers agree very well for all groups, except for the 9:3:4 ratios. Since the expected and observed numbers agree fairly well for all other groups, these deviations may not be significant. The results indicate that two genetic factors are involved in the development of color in the apexes.

TABLE 10.—*Segregation of F_2 progenies from the cross Niro Vialone × Caloro for color of lemma and palea apexes, at Biggs, Calif., 1925*

Color group of F_2 progeny and number of families	F_2 progenies having apexes—			Deviation from 3:1 ratio, and probable error
	Purple	Red	Green	
Purple leaves, leaf sheaths, and lemma and palea apexes:				
4	483			
3	226		64	−8.50±4.97
4	342	126		+9.00±6.32
7	408	121	222	
Expected in a 9:3:4 ratio [a]	422.44	140.81	187.75	
Deviation	−14.44	−19.81	+34.25	
Purple-striped leaves and leaf sheaths, and purple lemma and palea apexes:				
5	379	128		+1.25±6.58
4	294	69	95	
Expected in a 9:3:4 ratio [b]	257.63	85.87	114.50	
Deviation	+36.37	−16.87	−19.50	
Green leaves, leaf sheaths, and lemma and palea apexes:				
14			1,471	
Green leaves and leaf sheaths with red awns and lemma and palea apexes:				
3		371	[c]1	
3		224	86	+8.50±5.14

[a] $\chi^2=9.5286$ $P=0.0088$.
[b] $\chi^2=11.7697$. $P=0.0028$.
[c] The seed producing this plant floated in during the first irrigation.

IN BUTTE × COLUSA

The Butte variety has reddish apiculi, whereas Colusa has green. In the cross Butte × Colusa the F_1 plants had red apiculi, but the adjacent tissues of the apexes were green.

F_2 PROGENY

In the F_2 progenies grown in 1925 there were 634 plants with red to 203 with green apiculi. These numbers are in close agreement with those expected in a 3:1 ratio. The deviation is only 6.25 plants, with a probable error of ±8.45. The data indicate that there is a single genetic-factor difference for color of the apiculi in this cross.

F_3 PROGENY

In F_3, 10 of the families bred true for red and 19 for green apiculi, just as they did for red and green awns, as was expected. However, 11 families segregated for red and green apiculi in F_3. There were 404 plants with red apiculi and 152 with green.

The segregation of nearly all families agreed very well with that expected in a 3:1 ratio. The deviation from the expected numbers in a 3:1 ratio was 13 plants, with a probable error of ±6.89. The observed and expected numbers are in close agreement, therefore, which indicates that one factor is involved in the production of red apiculi in the rices here studied. Apparently the same genetic factor is responsible for red apiculi and red awns in this cross.

IN COLUSA × ITALIAN RED

Colusa normally has no color in any of its organs. In Italian Red many of the organs, including the lemma and palea apexes, are purplish. In the cross Colusa × Italian Red the lemma and palea apexes were purple in the F_1. The F_2 plants were separated into three groups, purple, red, and green. The results are shown in Table 11. The observed numbers of plants agreed very well with the expected numbers for each color group. The deviation from the numbers expected in the 9:3:4 ratio is very small in each group. These data indicate that two independently inherited factors account for the production of color in the lemma and palea apexes in this case.

IN C. I. 5346 × ITALIAN RED

Data on the segregation of F_2 plants of the cross C. I. 5346 × Italian Red for color of the lemma and palea apexes are presented in Table 11.

TABLE 11.—*Segregation of F_2 hybrids from the crosses Colusa × Italian Red, and C. I. 5346 × Italian Red, and from both crosses and from the cross Niro Vialone × Wataribune, for color of lemma and palea apexes, at Biggs, Calif., 1926*

Cross and color group	Number of plants		Deviation	x^2	P
	Observed	Expected in 9:3:4 ratio			
Colusa×Italian Red:					
Purple	291	288	+3	0.2683	0.8944
Red	98	96	+2		
Green	123	128	−5		
C. I. 5346×Italian Red:					
Purple	259	289.125	−30.125	7.2278	.0275
Red	111	96.375	+14.625		
Green	144	128.500	+15.500		
Total from both crosses:					
Purple	550	577.125	−27.125	3.1414	.2107
Red	209	192.375	+16.625		
Green	267	256.500	+10.500		
Niro Vialone×Wataribune:					
Purple	286	264.375	+21.625	11.1046	.0039
Red	60	88.125	−28.125		
Green	124	117.500	+6.500		

It will be observed that the deviations from the expected numbers in a 9:3:4 ratio are larger than for the progeny of Colusa × Italian Red. The deviation for the purple group is negative and relatively large. These F_2 plants were classified when they were nearly all mature, and it is quite probable that on some of the plants the purple color of the lemma and palea apexes had faded to such an extent that they were not correctly classified, as both the red and the green groups have rather large plus deviations. The writer often has observed that the purple or red color in various plant organs may disappear almost entirely when the plants reach maturity, and for this reason it is very difficult to classify correctly an F_2 population late in the season. The results indicate, however, that two independent genetic factors probably are responsible for color in the lemma and palea apexes.

In Table 11 are combined the results of F_2 segregation for color of lemma and palea apexes in both crosses. The combined numbers agree very well with those expected in a 9:3:4 ratio. This indicates that color in the lemma and palea apexes of Italian Red rice is due to two independently inherited genetic factors. The data indicate that the factorial constitution with respect to color of lemma and palea apexes is *CP* for the Italian Red variety and *cp* for Colusa and C. I. 5346.

IN NIRO VIALONE × WATARIBUNE

In Niro Vialone nearly all the organs are purplish, whereas in Wataribune none is colored. In the cross of these two, purple lemma and palea apexes were dominant in F_1. Segregation in F_2 resulted in a ratio of about 9 plants with purple lemma and palea apexes to 3 plants with red to 4 plants with green, as shown in Table 11. The deviation from this ratio may be significant, for the value of *P* indicates a rather poor fit.

IN EUREKA × CALORO

Eureka has no colored organs except the apiculi, which are red. All the organs of Caloro are without color. In the cross between these two varieties the F_1 plants had red apiculi. The segregation of F_2 plants resulted in approximately 3 plants with red to 1 with green apiculi. From certain segregating F_3 families there again were obtained approximately 3 plants with red apiculi to 1 with green, thus verifying the correctness of the monohybrid ratio. However, in two F_3 families, there were two types of red apiculi. In one the red developed early, that is, as soon as the plants began to head; whereas in the other the apiculi were green until the spikelets began to ripen. Then the apiculi assumed a brick-red color. In these two families the ratio of red to brick red was 3:1.

COLOR OF INTERNODES, GLUMES, AND STIGMAS

The internodes in rice usually are green, but in some varieties they are colored. Parnell and others (*13*) reported that in a cross of a variety having golden internodes with one having green, golden was recessive to green, and in F_2 there were 3 plants with green internodes to 1 with golden. He attributed the dominance of the green color in this case to the action of a factor which inhibited the appearance of the golden color. In another cross Parnell and his associates found that purple internodes were dominant in F_1 and that segregation in F_2 produced 3 plants with purple internodes to 1 with green.

Hector (*3*) found that colored internodes and stigmas were dominant to green in F_1, and that segregation in F_2 occurred in ratios of 3:1, 9:7, and 27:37 colored to green plants, respectively. In one case Hector (*2*) found that stigma color was due to the interaction of four dominant complementary factors giving in F_2 81 plants with colored stigmas to 175 with green. He found also that colored glumes were dominant over green in F_1, and that in the F_2 progenies ratios of 3 plants with colored glumes to 1 with green, or 9 with colored to 7 with green, were obtained. Ikeno (*5*) reported a 3:1 ratio in F_2 for plants with colored and green stigmas. These data indicate that color in the internodes and stigmas may be due to the action of one genetic

factor, or to the interaction of two or three dominant complementary factors, while color in the glumes may be due to a single genetic factor or to complementary factors.

IN NIRO VIALONE × CALORO

In Niro Vialone, it will be remembered, nearly all the organs, including the three under discussion, are purple or purplish. In Caloro, on the other hand, all the organs are green. In the cross between Niro Vialone and Caloro the F_1 hybrids had purple internodes, glumes, and stigmas.

F_2 PROGENY

Segregation in F_2 produced two groups, consisting of 115 plants with purple internodes, glumes, and stigmas and 92 plants with these organs green. The numbers expected in a 9:7 ratio are 116.44 and 90.56, respectively. The deviation is 1.44 plants, with a probable error of ±4.81.

F_3 PROGENY

The purple group consists of phenotypic classes 1 and 4, and the green groups of phenotypic classes 2, 3, 5, 6, 7, and 8. In F_3 progenies from the purple group some families should breed true for purple internodes, glumes, and stigmas, while others should segregate in the ratio of 3 plants with these organs colored to 1 with organs green, and 9 with colored organs to 7 with green. Families in the green group, regardless of genetic constitution, should breed true in F_3, and this result was obtained in 20 families, consisting of 2,153 plants. The results are shown in Table 12.

TABLE 12.—*Segregation of F_3 progenies from the cross Niro Vialone × Caloro for color of internodes, glumes, and stigmas, at Biggs, Calif., 1925*

Color group of F_2 progeny and number of families	F_3 progenies having internodes, glumes, and stigmas—		Deviation from 3:1 ratio, and probable error	Deviation from 9:7 ratio, and probable error
	Purple	Green		
Purple leaves and leaf sheaths, internodes, glumes, and stigmas:				
4	483			
7	568	190	+0.50±8.04	
7	405	349		+19.13±9.19
Purple-striped leaves and leaf sheaths, and purple internodes, glumes, and stigmas:				
6	487	153	−7.00±7.39	
3	185	140		−2.19±6.03
Green leaves and leaf sheaths, and green leaves and leaf sheaths with red apexes, both groups with green internodes, glumes, and stigmas:				
20		2,153		

An inspection of Table 12 shows that in the families from class 1 of the purple group four families contained only individuals with purple organs, and that the observed and expected numbers for the 3:1 and 9:7 ratios are in excellent agreement. One expected ratio is lacking, however, for there should be some families which in segregation would produce 3 plants with purple internodes, glumes, and stigmas to 1 with those organs red. No plants with red internodes, glumes,

and stigmas were detected in F_3, however. It is possible that such plants were present and that the red color was so dilute that it escaped detection. In this event the red plants would be classed as green, but as all plants were carefully classified this hardly seems possible. This particular segregation is lacking also from class 4 of the purple group.

No true-breeding purple progenies were obtained in F_3 from class 4 of the purple group, but true-breeding strains were present in F_4. Six of the nine segregating F_3 progenies from class 4 produced about 3 plants with purple internodes, glumes, and stigmas to 1 plant with green. The other three families produced plants in the ratio of 9 purple to 7 green, as shown in Table 12. The observed and expected numbers for these ratios in F_3 are in very good agreement.

The data herein presented on the inheritance of color of the internodes, glumes, and stigmas, in the cross Niro Vialone × Caloro, are in general agreement with the 3-factor hypothesis. The colors of internodes, glumes, and stigmas in this case apparently are due to the same dominant complementary genetic factors or to completely linked factors.

IN COLUSA × ITALIAN RED

Colusa has no colored organs, but Italian Red rice has internodes with purplish color extending up and down the culms for a short distance from the nodes. In the cross Colusa × Italian Red the F_1 plants have purple internodes, and in F_2 there were 226 plants with purple internodes to 280 with green internodes. These numbers agree very well with a Mendelian 27:37 ratio. The deviation from the expected numbers is 12.53 ± 7.49 plants.

The F_1 plants from this cross also had purplish color in the glumes and stigmas. The segregation in F_2 produced 292 plants with purple glumes and stigmas to 222 with green. The deviation from the expected numbers in a 9:7 ratio is 2.875 plants with a probable error of ± 7.59, which indicates a very good fit.

Attention should be called to the fact that in the cross Niro Vialone × Caloro the color of the internodes, glumes, and stigmas was inherited as a unit, whereas in the cross Colusa × Italian Red the color in the internodes appears to be due to three complementary factors and that in the glumes and stigmas to two complementary factors.

IN NIRO VIALONE × WATARIBUNE

The variety Niro Vialone, having nearly all organs purple, and the variety Wataribune, having all organs green, were crossed. In this cross the F_1 plants had purple internodes, and segregation in F_2 produced 286 plants with purple internodes to 184 with green ones. These numbers are in fair agreement with those expected in a 9:7 ratio. The results presented indicate that color in the internodes of the rices studied apparently is due to the presence of two or three dominant complementary factors.

COLOR OF NODES, LIGULES, AURICLES, AND PULVINI

In rice the nodes, ligules, auricles, and pulvini usually are green. In some varieties these organs are colored, however. Hector (*3*) found in rice crosses that color in the ligules, auricles, and pulvini was

dominant to green in F_1, and that segregation in F_2 resulted in approximately 9 plants with these organs colored to 7 in which they were green. He also reports in the F_2 segregation of one cross a ratio of 27 plants with colored ligules to 37 with green. These results indicate that color in the ligules, auricles, and pulvini of the rice studied by Hector was due to the interaction of two dominant complementary genetic factors, and that in one case ligule color was due to the interaction of three dominant factors. Parnell and others (*13*) found that purple color in auricles and pulvini was dominant in F_1 and that segregation in F_2 produced three plants with purple auricles and pulvini to one with green.

A great deal of difficulty is experienced in studying the inheritance of color of nodes in rice. In California the nodes of the rice culms often remain inclosed by the leaf sheaths from the next lower nodes and, therefore, are not exposed to the direct rays of the sun. Exposure to the sun appears to be necessary, however, for the proper development of color in the nodes; therefore errors in classification scarcely can be avoided, even if the sheaths are removed and the naked nodes studied.

IN NIRO VIALONE × CALORO

Niro Vialone has purple nodes, ligules, auricles, and pulvini, whereas Caloro has no colored organs. In the F_1 hybrid from the cross Niro Vialone × Caloro all of these organs were purple.

F_2 Progeny

Segregation in F_2 resulted in 100 plants with these organs purple to 107 plants with them green. The numbers calculated for a 27:37 ratio are 87.53 and 119.67, respectively, and the deviation is 12.67 plants, with a probable error of ± 4.79. The deviation therefore is somewhat less than three times the probable error, which indicates a satisfactory fit.

F_3 Progeny

The purple group consists of phenotypic class 1, and the green group of phenotypic classes 2 to 8, inclusive. On a 3-factor basis some of the purple-group progenies should breed true in F_3 and others should segregate in ratios of 3 purple plants to 1 green, 9 purple plants to 7 green, and 27 purple plants to 37 green. All F_3 progenies from the green group should and did breed true, 20 families, containing 2,153 plants, being tested in this group. The data on F_3 progenies are presented in Table 13.

Of the 18 F_3 progenies from the purple group 4, consisting of 483 plants, bred true for purple nodes, ligules, auricles, and pulvini. Three progenies segregated in the ratio of 3 plants with these organs purple to 1 with green. Eight progenies segregated in the ratio of 9 with purple to 7 with green, and 3 progenies segregated in the ratio of 27 with purple to 37 with green. Nine F_2 families having purple-striped leaves and leaf sheaths and green nodes, ligules, auricles, and pulvini, consisting of 965 plants, bred true for green nodes, ligules, auricles, and pulvini.

TABLE 13.—*Segregation of F_3 progenies from the cross Niro Vialone × Caloro for color of nodes, ligules, auricles, and pulvini, at Biggs, Calif., 1925*

Color group of F_2 progeny and number of families	F_3 progenies having nodes, ligules, auricles, and pulvini—		Deviation from 3:1 ratio, and probable error	Deviation from 9:7 ratio, and probable error	Deviation from 27:37 ratio, and probable error
	Purple	Green			
Purple leaves, leaf sheaths, nodes, ligules, auricles, and pulvini:					
4	483				
3	259	103	+12.50±5.56		
8	475	370		+0.31±9.73	
3	137	168			+8.33±5.82
Purple-striped leaves and leaf sheaths and green nodes, ligules, auricles, and pulvini:					
9		965			
Green leaves and leaf sheaths, and green leaves and leaf sheaths with red apexes, both groups with green nodes, ligules, auricles, and pulvini:					
20		2,153			

An inspection of Table 13 shows that the observed and expected numbers for each of the three ratios are in excellent agreement, which indicates that for the color of nodes, ligules, auricles, and pulvini, the 3-factor hypothesis fits the results. Color in these four organs in this case apparently is due to the interaction of three dominant complementary factors. The color in all four organs is inherited as a unit, and the color of each apparently is due to the same genetic factor or factors in the variety here studied.

The data presented in the preceding pages on the inheritance of color in the cross Niro Vialone × Caloro were found, as a whole, to warrant the 3-factor hypothesis. A few ratios that were expected in F_3 were not obtained, but this probably was due to the limited number of F_3 progenies grown and to the large number of characters studied. One true-breeding type not obtained in F_3 was found to be present in the F_4 selections. The deviation from the expected ratio in F_3 was in one case very large, and no doubt significant, but in nearly all other cases the observed and expected numbers were in fairly good agreement. In a study of so many characters a much larger number of F_3 families and plants should have been used, but this was not possible because of the shortage of land and labor. It is felt, however, that the data presented, while not extensive, have been in harmony with the 3-factor hypothesis.

Color in the rice plant was found by Hector (*3*) and Nagai (*12*) to be inherited by groups of organs. In the cross Niro Vialone × Caloro, likewise, the color characters of the Niro Vialone parent, as has been noted, were inherited in groups as if the colors were due to the action or interaction of the same genetic factors or to completely linked factors. In this cross color was inherited by four groups of organs, namely: (1) Leaves and leaf sheaths; (2) awns and lemma and palea apexes; (3) internodes, glumes, and stigmas; and (4) nodes, ligules, auricles, and pulvini. The colors of all organs within each group were inherited in the F_2 and F_3 generations as if they were due to the same genetic factors or to completely linked factors, but no evidence was found in support of completely linked factors.

IN COLUSA × ITALIAN RED

Colusa has no colored organs, whereas Italian Red has purple color in all the organs under consideration. In this cross the F_1 plants had culms with purple nodes. Of the F_2 plants, 254 had purple nodes and 253 had green nodes. These numbers, being almost equal, represent practically a perfect 1:1 ratio, but such a ratio is not to be expected from an F_1 population in which purple nodes were dominant. It is very possible, therefore, that some of the F_2 plants classed as having green nodes would have developed color in the nodes with longer exposure to the sun. This probably would have resulted in a 9:7 ratio with purple nodes dominant.

In the cross Colusa × Italian Red the colors of the ligules, auricles, and pulvini were inherited as if they were due to the same factors or to completely linked factors. There were 269 F_2 plants with purple ligules, auricles, and pulvini to 244 with these organs green. These numbers are in fairly good agreement with a 9:7 ratio. The deviation from the expected numbers in a 9:7 ratio is 19.56 plants with a probable error of ±7.58. The deviation probably is not significant, for it is less than three times the probable error. The purple color in these organs apparently is due to the complementary action of two dominant genetic factors, both of which are necessary for the production of the color.

IN NIRO VIALONE × WATARIBUNE

In the plants from a cross between Niro Vialone and Wataribune grown at Biggs, the nodes were colored in F_1. Niro Vialone has purplish and Wataribune green nodes. Of the F_2 plants, 258 had purple nodes and 212 had green. This is in close agreement with the numbers expected in a 9:7 ratio. The deviation from the expected is 6.375 plants, with a probable error of ±7.25.

COLOR OF SEED COATS

The color of the seed coats, as seen in hulled kernels of rice, may be white, brown, red, purple, or purplish black. White, or brown of various shades, are the most common colors. Red rice is present in most rice-growing countries, but purple rice is rather uncommon.

Red rice derives its name from the red color of the outer seed coats, visible in hulled kernels. The intensity of the color depends, for a given variety, upon the stage of maturity of the rice. Usually only well-matured kernels are fully red. There probably are varieties of rice which represent each shade of kernel color between white and dark red. In most red varieties the color is confined to the surface coats of the kernels. The color in some red rices appears, however, to extend into the pericarp.

The inheritance of red color in rice kernels has been studied by several workers. Hector (*1*) and Parnell and others (*13*, *14*) in India, McKerral (*11*) and Thompstone (*17*) in Burma, Van der Stok, according to McKerral (*11*), in Java, Ikeno (*5*) and Kato and Isikawa (*8*) in Japan, and Jacobson (*6*) in the Philippines, all reported that red color is dominant in F_1 and that Mendelian ratios of 3 red-kerneled plants to 1 white-kerneled plant occur in F_2 or later generations.

Parnell and others (*13*, *14*), in a study of the inheritance of color in rice, found F_2 ratios of 3 colored-kerneled plants to 1 white-ker-

neled and of 9 red-kerneled plants to 3 gray-brown to 4 white-kerneled ones. Kato and Isikawa (*8*) also reported, in the F_2 of one cross, a ratio of 3 red-kerneled plants to 1 white-kerneled. In another cross, using the same red female parent, but a different white male parent, they found that the segregation in F_2 was in the ratio of 9 plants having red kernels to 3 having yellowish-brown kernels to 4 having white kernels. Nagai (*12*), in a cross of a variety having pale-buff (white) kernels with one having reddish-brown kernels, reported segregation in F_2 in the ratio of 9 reddish-brown to 3 yellow-brown to 4 pale-buff (white) plants. Kato and Isikawa (*8*) also found that the reddish and yellowish-brown pigments in the rices studied by them belong to the protocyan and not to the anthocyan group of pigments.

IN COLUSA × ITALIAN RED AND C. I. 5346 × ITALIAN RED

Colusa and C. I. 5346 have no colored organs, whereas Italian Red has purplish color in most organs and has red seed coats. Three F_1 plants of the cross Colusa × Italian Red and seven F_1 plants of the cross C. I. 5346 × Italian Red were grown to maturity. The F_1 plants of both crosses appeared to be more vigorous than the parent varieties. The Colusa variety matured from September 27 to 29, C. I. 5346 September 23 to 24, and Italian Red September 20 to 21. The F_1 plants of Colusa × Italian Red matured September 23, and those of C. I. 5346 × Italian Red September 21. The F_1 plants of both crosses, therefore, matured more nearly with the early parent.

The F_1 plants of the crosses Colusa × Italian Red and C. I. 5346 × Italian Red had color in all the organs that normally are colored in the male parent, though in most of the parts the color was less highly developed. The nodes, lemma and palea apexes, and awns were nearly as highly colored, and the hulled F_1 kernels were nearly as red, as in the male parent.

F_2 PROGENY

The counts on kernel color in the crosses studied were made late in October, when nearly all F_2 plants were well matured. A few very late F_2 plants did not mature well enough to make possible a classification of the color of the kernels, for the red color of the hulled kernel is not fully developed in California except in well-matured rice. The color of the kernels of the mature F_2 plants varied from white through pale red to dark red. It is probable that the dark-red kernels were on homozygous F_2 plants, and those with the lighter shades of red were on heterozygous F_2 plants. In these crosses all red kernels, regardless of the intensity of the red color, were classed as red.

In the cross Colusa × Italian Red there were 381 F_2 plants with red kernels to 120 F_2 plants with white kernels. These numbers are in close agreement with the Mendelian 3:1 ratio. The deviation from the ratio of 3 red to 1 white is only 5.25 plants, with a probable error of ± 6.54.

In the cross C. I. 5346 × Italian Red there were 400 F_2 red-kerneled plants to 125 with white kernels. These numbers also are in close agreement with a 3:1 ratio, with red-kernel color dominant. The deviation from a 3:1 ratio in this case is 6.25 plants and the probable error ± 6.69. The segregation in F_2 for both crosses gave a total of 781 plants with red seeds to 245 plants with white seeds,

which is in very close agreement with the Mendelian monohybrid 3:1 ratio. The deviation from the expected number in a 3:1 ratio is only 11.5 plants, with a probable error of ±9.36. It appears therefore that the red-kerneled and white-kerneled rices used as parents in these crosses differ by only a single genetic factor.

SUMMARY

In the crosses Niro Vialone × Caloro, Butte × Colusa, Colusa × Italian Red, Eureka × Caloro, and an unnamed variety C. I. 5346 × Italian Red, all organs that were colored in the Niro Vialone, Butte, Eureka, and Italian Red varieties were colored in the F_1 hybrids.

In F_2, segregation for purple color of the leaves and leaf sheaths, in the cross Niro Vialone × Caloro, produced numbers fairly close to a 27:9:28 ratio. In F_3, the green strains bred true and the purple strains either bred true or segregated according to their genetic constitution in 3:1, 9:7, or 27:9:28 ratios. In the 27:9:28 ratio the fit was poor.

The F_2 segregation for color of the awns and lemma and palea apexes in the crosses Niro Vialone × Caloro, Colusa × Italian Red, and C. I. 5346 × Italian Red produced numbers agreeing with a 9:3:4 ratio. In F_2, Niro Vialone × Wataribune produced plants with purple, red, and green lemma and palea apexes in the ratio of approximately 9:3:4. The Butte × Colusa cross segregated in F_2 for color of both awns and apiculi in a ratio of 3 red to 1 green. The correctness of the last ratio was verified by growing F_3 progenies. In F_3 segregation, in the cross Niro Vialone × Caloro, the green strains bred true and the colored strains either bred true or segregated in 3:1 or 9:3:4 ratios.

The F_2 segregation in the cross Niro Vialone × Caloro for color of the internodes, glumes, and stigmas was in a 9:7 ratio of purple to green. In F_3 the green strains bred true and the purple strains either bred true or segregated in 3:1 or 9:7 ratios. The F_2 segregation in the cross Colusa × Italian Red produced plants with purple and green internodes in a 27:37 ratio and plants with purple and green glumes and stigmas in a 9:7 ratio. The F_2 segregation in the cross Niro Vialone × Wataribune produced plants with purple and green internodes in a 9:7 ratio.

The F_2 segregation in the cross Niro Vialone × Caloro for color of the nodes, ligules, auricles, and pulvini produced plants with these organs purple and green in the ratio of 27:37. In F_3 the green strains bred true and the purple strains either bred true or segregated in 3:1, 9:7, or 27:37 ratios. The F_2 segregation in the cross Colusa × Italian Red for color of the ligules, auricles, and pulvini produced plants with these organs purple and green in a 9:7 ratio, while the plants with purple nodes and those with green appeared in about equal numbers. The F_2 segregation in the cross Niro Vialone × Wataribune for color of nodes produced plants with purple and green nodes in the ratio of 9:7.

In the cross Niro Vialone × Caloro the colors of the four groups of colored organs—leaves and leaf sheaths; awns and lemma and palea apexes; internodes, glumes, and stigmas; and nodes, ligules, auricles, and pulvini—were inherited separately. Color in each group was inherited as a unit, however, and as if it were due to the same genetic factors or to completely linked factors. The results indicate that it is due to the same and not to completely linked factors.

The data presented indicate that with respect to the colored vegetative organs the Niro Vialone parent has the dominant complementary factors *ACP* and the Caloro parent the recessive factors *acp*. The interaction of these three factors gives the colors observed in the four groups of organs mentioned above. No color develops in the absence of factor *C*.

In the cross Colusa × Italian Red, the color of the awns, of the lemma and palea apexes, of the glumes and stigmas, and of the ligules, auricles and pulvini, was inherited in each group of organs as if it were due to the same genetic factors or to completely linked factors. The color of awns and apiculi and of lemma and palea apexes in the crosses Butte × Colusa and C. I. 5346 × Italian Red also was inherited as a unit.

Purple color in the organs studied was found to be bigenic; that is, two (or more) factors acting together were necessary for the production of purple color in all organs.

The F_2 segregation, in the crosses Colusa × Italian Red and C. I. 5346 × Italian Red, for color of the seed coats, as seen in hulled kernels, produced approximately 3 red-kerneled plants to 1 white-kerneled plant.

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THE COMPARATIVE NUTRITIVE VALUE OF YELLOW CORN AND THE GRAIN SORGHUMS HEGARI AND YELLOW MILO [1]

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INTRODUCTION

The sorghum grains are of great economic importance in the arid Southwest. They are immigrant crops, native to South Africa, which have proved themselves to be well adapted for growth in the southwestern plains, for they are drought resistant and high yielding with a minimum amount of water (*19*).[2] For this reason they are widely used in animal feeding rations in place of yellow corn, which can not be successfully grown in the drier regions (*11*).

Dissatisfaction has frequently accompanied the use of the sorghum grains as substitutes for yellow corn in farm-animal rations, the stock feeders thereby losing confidence in the nutritive value of these grains. Reports of "nutritional roup" in poultry following the use of these grains in Arizona are numerous. As a part of a hog-feeding investigation conducted by the Arizona Agricultural Experiment Station,[3] ground hegari was compared with yellow corn in the feeding of two lots of pigs for a period of 21 weeks. The pigs fed the corn were reported thrifty and vigorous, whereas those receiving the hegari showed evidences of some nutritional deficiency, failed to conceive, and became deaf and blind. These results, however, have not been duplicated in later experimental work.

Only a very limited number of tests of the nutritive value of the grain sorghums have been reported, the most recent and comprehensive being the study of the chemical and nutritive properties of a wide range of sorghum grains conducted by Heller and Green at the Oklahoma experiment station in 1925 (*3*). The present paper reports further upon the comparative nutritive value of yellow corn and the grain sorghums hegari and dwarf yellow milo.

EXPERIMENTAL DATA

CHEMICAL ANALYSES

Selected samples of hegari, dwarf yellow milo, and yellow corn were supplied by the agronomy department of the University of Arizona. The hegari and milo were grown on the university experimental farm and the yellow corn in Riley County, Kans. The results of routine chemical analyses of samples of the three grains used appear in Table 1.

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[1] Received for publication July 24, 1929; issued June, 1930.

[2] Reference is made by number (italic) to "Literature cited," p. 1144.

[3] WILLIAMS, R. H., BURNS, R. H., and SMITH, C. A. Unpublished data. Department of Animal Industry, University of Arizona. 1923.

TABLE 1.—*Percentage analyses of air-dry samples of hegari, dwarf yellow milo, and yellow corn*

Grain	Moisture	Ash	Fat	Protein	Carbohydrates (by difference)
Hegari	6.88	1.76	3.15	13.16	75.05
Dwarf yellow milo	6.64	1.78	3.37	13.87	74.34
Yellow corn	7.00	1.58	5.50	10.98	74.94

The figures in Table 1 do not differ materially from those of the United States Department of Agriculture (*11*). Drier air conditions in Arizona make an apparent higher protein, fat, and ash percentage of all the grains.

It is evident that chemical analysis gives no explanation of the observed superiority of yellow corn in the feeding of farm animals. The grain sorghums are distinctly higher than yellow corn in protein and lower in fat. The advantage of their higher protein content is, however, probably offset by a lower coefficient of digestibility (*1*). It may be that the higher fat content of the yellow corn is paralleled by a higher concentration of the fat-soluble vitamins and that this gives corn a distinct advantage over the sorghum grains.

ANIMAL-FEEDING EXPERIMENTATION

Unless otherwise indicated, all of the animals used in the following studies of the feeding value of the sorghum grains were of known nutritional history. They were taken from the stock colony of albino rats reared on Sherman's diet B, composed of two-thirds ground whole wheat, one-third whole milk powder, and sodium chloride equal to 2 per cent of the weight of the wheat, with fresh lettuce given daily. At the time of weaning (28 to 29 days) litter mates, matched as to size and sex as far as possible, were placed upon the different experimental rations. The living conditions of all the animals were identical, the animals being reared in square metal cages with false screen bottoms which were changed daily. Not more than three males and three females were kept in one cage. The experimental rations and distilled water were fed ad libitum. Weekly records of the weights of the animals and their food intake were kept, and a close observation of all the animals made, and all abnormalities recorded.

Pregnant females were separated from the lot and weighed every other day until their litters arrived, at which time their weights were again recorded. Bedding for the young consisted of finely cut white crêpe paper. The young were weighed as a lot weekly until they were 4 weeks old, at which time they were weighed separately, numbered and recorded as individuals, and the mother returned to the lot from which she came. For the purpose of studying the effect of the ration upon the succeeding generations, one pair of young from the first litter of each female was continued upon the diet of the mother.

Criteria for comparing the adequacy of the experimental rations consisted of such health factors as rapidity of growth, maximum size attained, age of maturity, success of reproduction and rearing of the young, physical vigor of parents and offspring, including duration of their prime of life (*13*, *14*, *15*, *16*).

The Sorghum Grains as the Sole Source of Nutriment

The inadequacy of cereal grains as the sole source of nutriment for animals has long since been recognized. In 1915, McCollum and

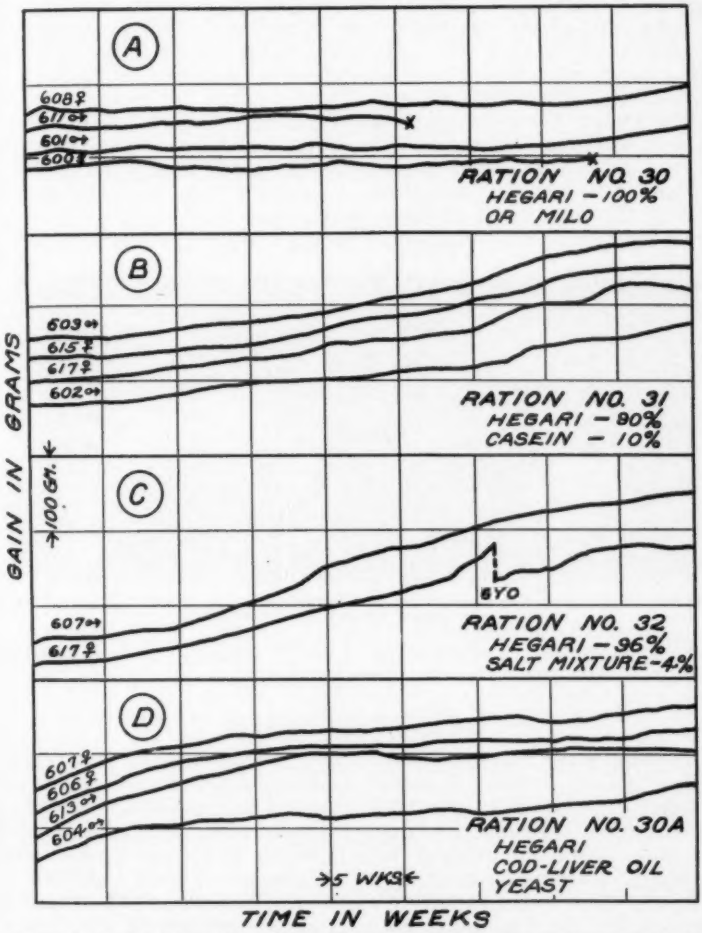

FIGURE 1.—Growth and reproduction records of representative animals receiving unsupplemented and supplemented hegari rations: A, Animals fed hegari or milo singly made no appreciable growth; B, growth response obtained by the addition of casein to the hegari ration; C, growth response obtained by the addition of Osborne and Mendel's salt mixture to the hegari ration; D, effect of supplementing hegari with cod-liver oil and yeast, in which case the slight growth response obtained may probably be due to the small amount of protein in the yeast

Davis (*6*) showed that wheat, oats, and corn when fed singly did not promote normal animal nutrition. Representative results of feeding hegari and yellow milo singly to albino rats from the time of weaning are shown graphically in Figure 1, A.

Both hegari and yellow milo are obviously deficient in dietary factors essential for growth or even continued maintenance through a normal life span. The animals in these groups made practically no gains in weight, nor showed much growth of the skeleton, and did not mature sexually. Two of the group died in the fifth and seventh months, respectively, and the others, though still living in the twelfth month, were in very poor physical condition. (Fig. 2.) On the other hand, when hegari is adequately supplemented, results such as appear in Figure 3 are obtained.

The growth performance of all the animals on ration 4 was superior to that of Donaldson's normal rat (*2*). The females matured early and produced four to five litters each during the 12 months of observation. The average size of the litters was 9.3. Ninety-two per cent of the young were successfully suckled and weaned at an average weight of 58 gm. No decline in health and vigor was seen in the

FIGURE 2.—Litter mates showing the effect of feeding hegari singly (left) and hegari suitably supplemented with protein, minerals, and vitamins (right)

fourth generation. Hegari when suitably supplemented apparently serves as a good basis for an adequate ration.

THE SORGHUM GRAINS AS SOURCES OF PROTEIN

McCollum and his associates (*5*, *7*, *8*, *9*) has shown that certain grains, including wheat, oats, rice, and corn are inadequate in protein content, probably lacking certain essential amino acids in sufficient concentration. Heller and Green (*3*) have more recently indicated that milo does not provide sufficient protein for normal growth and, like corn, is incomplete in amino acid make-up. That protein is likewise a limiting factor in hegari is evident from the growth response obtained by the single addition of purified protein to the hegari ration (fig. 1, B), growth being resumed though at a subnormal rate when purified casein was added to the diet.

When hegari was fed as the chief source of protein in a diet which contained all other known dietary essentials, results such as appear in Figure 4 were obtained. Not only did the animals dependent upon 92 per cent hegari for their protein (ration 36) [3] grow at a subnormal rate, but they reached maturity slowly. Some reproduction took place, but suckling of the young was markedly unsuccessful.

[3] The small amount of protein in the yeast probably made the protein deficiency of hegari less apparent.

Of the 43 offspring born to two females during the period of observation, all but six died and were eaten by their mothers in the first and second week. The young that lived were capable of but very slow subsequent growth. They were undersized, weighing only 18 to 22 gm. at weaning, appeared well nourished though small, and

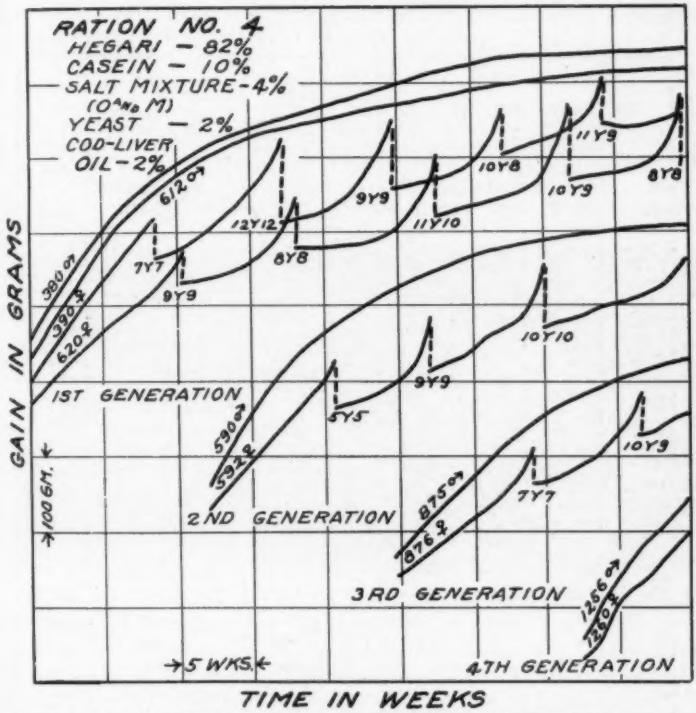

FIGURE 3.—Growth and reproduction records of representative animals receiving hegari adequately supplemented with protein, minerals, and vitamins. Growth at an optimum rate, health and vigor, and a high degree of success in reproduction and lactation resulted. Four generations were obtained in the year of observation. Each generation exhibited optimum growth and reproduced and reared young in their turn fully equal to the average. The break in the curves of females represents loss in weight upon parturition. The numeral before the Y indicates the number of offspring and that after the Y the number of young weaned

possessed the long lithe form that is characteristic of the stunting due to insufficient protein in the diet. (Fig. 5.)

THE SORGHUM GRAINS AS SOURCES OF MINERAL ELEMENTS

The meager growth acceleration resulting from the addition of protein to the ration of animals that had become stationary in weight when hegari was fed singly, suggested that protein is not the sole limiting factor of the sorghum grains. As early as 1889, Henry (*4*) noted the deficiency of the corn kernel in mineral elements. Since that time McCollum and his coworkers (*5*, *7*, *8*, *9*) has demonstrated a deficiency of calcium, chlorine, and sodium in wheat, oats, rice, corn, and other seeds.

In Figure 1, C, may be seen the effect of feeding Osborne and Mendel's (*10*) salt mixture to animals that remained stationary in weight on the 100 per cent hegari ration. An immediate resumption of growth followed the addition of this mixture to the ration, though again the growth rate was below normal, due to other limiting factors. When hegari (86 per cent) served as the sole source of mineral elements in a diet which was otherwise complete (ration 33), data such

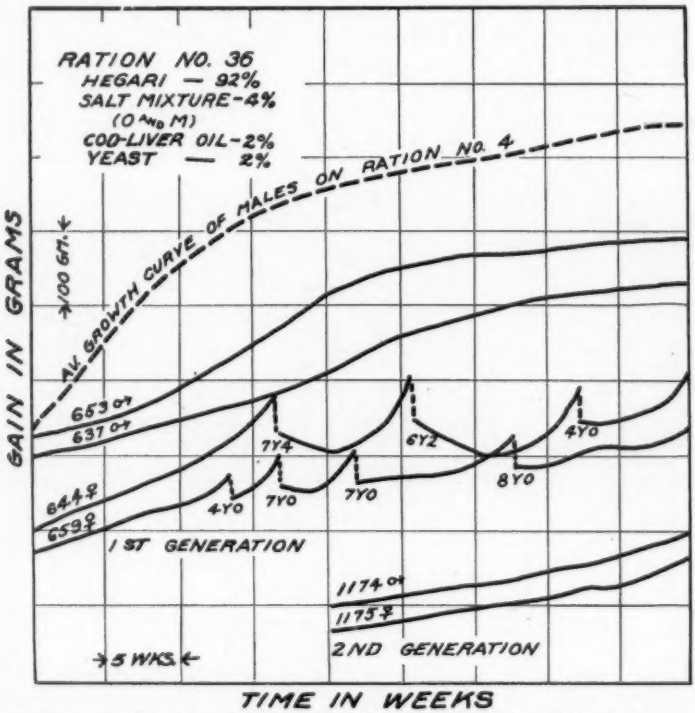

FIGURE 4.—Growth and reproduction records of representative animals receiving hegari as the chief source of protein in an otherwise complete ration; the growth rate is subnormal and reproduction highly unsuccessful

as appear in Figure 6 were obtained. All of the animals in this group made far less than normal weekly gains. Attainment of sexual maturity was delayed, and again reproduction and lactation were highly unsuccessful. Only 3 of 16 young born to 2 females were weaned and these were runts, weighing but 20 to 23 gm. Abnormal development of the skeleton was apparent, the animal presenting a short stocky appearance in contrast to the long lithe form of the normal or protein-stunted animals.

When sodium and chlorine were included in the ration in the form of 1 per cent sodium chloride (ration 38), growth was strikingly

accelerated and the reproduction record improved, though perfectly normal reproduction and lactation were not observed. (Fig. 7, A.) A more nearly optimum response, however, was obtained by the further addition of 1 per cent calcium lactate (ration 39), as shown in Figure 7, B. Undoubtedly hegari is deficient in calcium and in sodium or chlorine or both, and these must be introduced into rations of which hegari comprises a large part if normal growth and normal reproductive performance are to be expected.

The Sorghum Grains as Sources of Vitamin A

On the basis of his studies of the nutritive value of wheat, barley, rice, oats, and corn, McCollum concluded that grains as a class are deficient in vitamin A and observed that vitamin A is concentrated in the more actively functioning part of the plant, that is, in the leaf or stem. On the other hand, Steenbock (*18*) has called attention to

Figure 5.—Litter mates showing the protein inadequacy of hegari when constituting 92 per cent of the ration. Note the long, lithe form and poor coat of the animal (left) which was fed hegari as its sole source of protein, and compare with its normal litter mate (right) fed hegari and an adequate protein supplement

the association of vitamin A with yellow pigmentation and has shown that yellow corn, though a plant-storage organ, is rich in vitamin A, whereas white corn is strikingly deficient in this vitamin. In 1925, Heller and Green (*3*) reported that the feeding value of the sorghum grains is comparable to that of yellow corn, that the vitamin A content of most of the group is sufficient for all practical purposes, being present in amounts sufficient for growth and reproduction but in all species insufficient for continued rearing of the young.

In Figures 8 and 9 are graphically presented the growth and reproduction records of litter mates taken from the stock colony in this laboratory at the time of weaning and placed on rations in which vitamin A was derived from 84 per cent ground hegari (ration 37) or yellow corn (ration 3), respectively.

In Table 2, the average gains in weight of the males reared on rations 37 and 3 are compared with those of animals which received additional vitamin A in the form of cod-liver oil. (Ration 4, fig. 3.)

TABLE 2.—*Average gains in weight of males on rations Nos. 37, 3, and 4*

FIRST GENERATION

Ration No.	Number of males	Average initial weight	Average gain in weight in grams in—							
			4 weeks	8 weeks	12 weeks	16 weeks	20 weeks	24 weeks	28 weeks	36 weeks
		Grams								
37	9	57	102	151	195	227	244	272	276	276
3	4	58	113	185	236	264	270	280	316	319
4	6	57	112	189	254	277	294	312	327	342

SECOND GENERATION

37	7	37	73	139	202	233	245			
3	6	51	98	149	219	236	267	295	290	
4	6	56	109	178	250	272	290	306	320	

THIRD GENERATION

37	2	32	74							
3	4	44	98	162	203	238	251			
4	6	58	115	182	253	275	298			

FOURTH GENERATION

37 [a]										
3	2	42	96	166						
4	4	57	113	186						

[a] No fourth generation on diet 37.

The rate of growth of the animals in both the unsupplemented hegari and corn groups is normal at first, the corn-fed animals, however, approaching the optimum growth rate more closely. The lot on hegari (ration 37) exhibits a greater slackening of the growth rate as adult size is approached, and none of the animals of the lot receiving additional vitamin A (ration 4) attain the maximum size for their age. It may be noted that growth in the successive generations on rations 37 and 3 was progressively more retarded, whereas the young of animals given a diet in which there was no lack of vitamin A showed no such slackening of the growth rate, even in the fourth generation.

As pointed out by Sherman and his associates (*13*, *14*, *15*, *16*), differences in size are not of such great significance as the "differences in vigor reflected by breeding records." Reproductive records for one-third of the normal life span of the first generation females on rations 37, 3, and 4 are given in Table 3.

TABLE 3.—*Reproductive records of first generation females on rations Nos. 37, 3, and 4*

Ration No.	Number of litters per female	Average size of litters	Average number of young per female	Average number of young weaned	Percentage of young weaned	Average weight of young at weaning
						Grams
37	4	7.0	28.0	15.0	53.6	37
3	5	9.6	48.0	35.0	73.0	51
4	5	9.6	43.2	39.5	91.8	56

Though there is practically no difference in the number of litters produced by each female, a difference in size of the litters and a more striking difference in the percentage of young successfully suckled and weaned may be noted. The females reared on hegari ration 37 gave birth to litters with an average size of 7 and weaned but 53.6 per cent of the young as compared with an average litter of 9.6 offspring with 91.8 per cent successfully suckled under the same rigorous living conditions by each female which had been given an

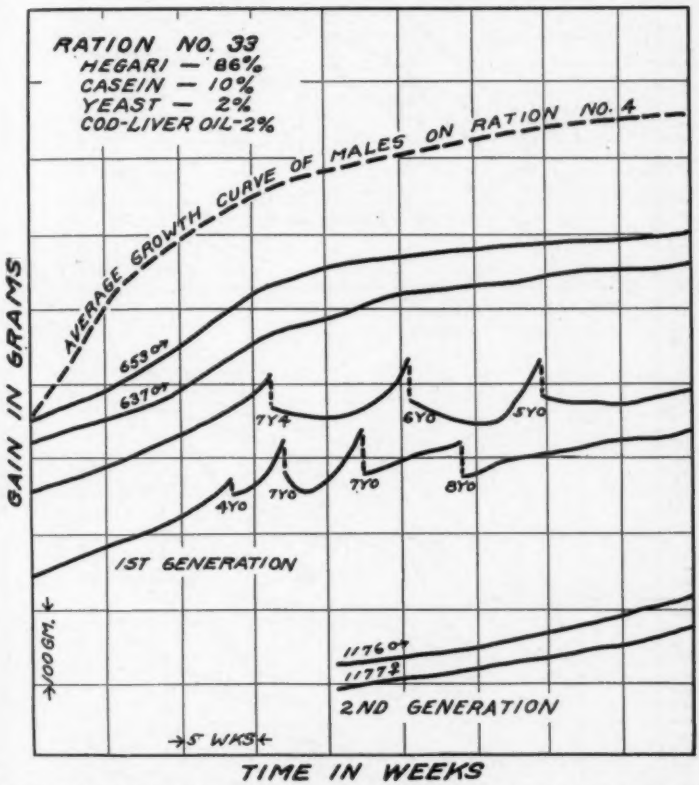

FIGURE 6.—Growth and reproduction records of representative animals receiving hegari as the chief source of mineral elements in an otherwise complete ration. All of the animals grew at a rate far below normal, reached sexual maturity slowly, and produced and raised but few young

additional source of vitamin A (ration No. 4). (Figs. 10 and 11.) It is also plain from Figure 8 that the percentage of young raised by each female on ration 37 falls sharply in the late litters, whereas no such corresponding drop in percentage reared is indicated in the records of females on ration 4, Figure 3. Continuing the animals on these rations for a longer period will therefore make this difference more striking, as a progressively smaller percentage of young weaned will be obtained in the group of animals dependent solely upon hegari for vitamin A. The difficulties of raising young and the

drain upon the mother rat were again indicated by the loss of her own body weight during the lactation period, as shown in Figure 7.

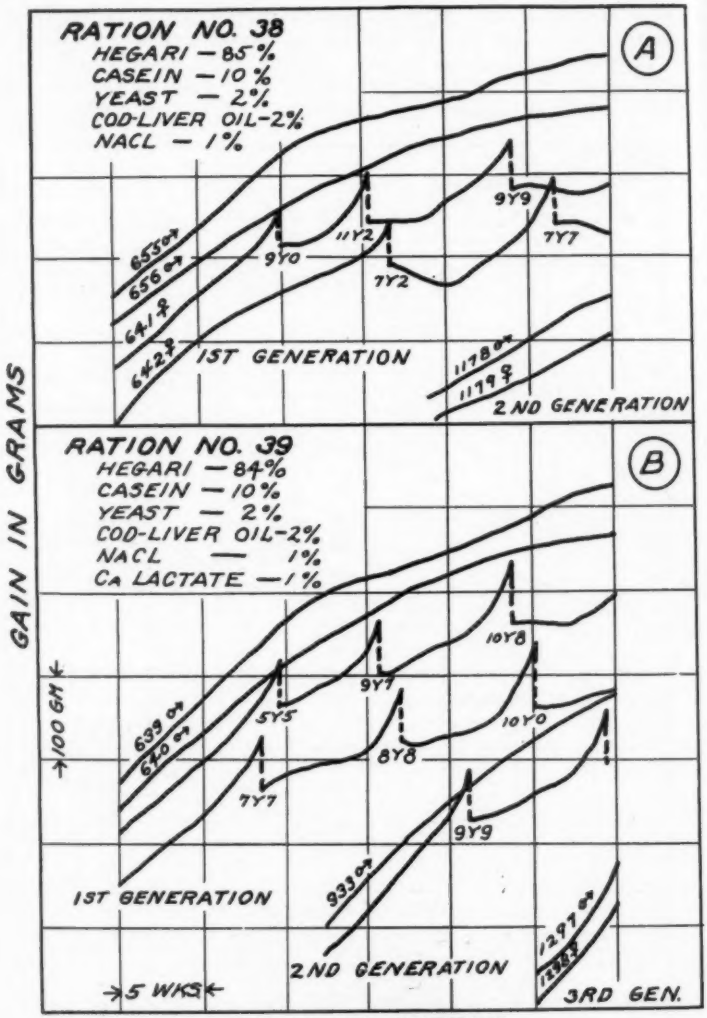

FIGURE 7.—A, Growth and reproduction records of representative animals that received sodium chloride in addition to hegari fed as the chief source of mineral elements in an otherwise complete ration; although marked improvement resulted from the inclusion of sodium chloride in the ration, perfectly normal reproduction was never obtained. B, The improved nutritional state of the animals on the further addition of calcium lactate to the ration indicates the deficiency of hegari in this respect

By these same criteria, we have further proof of the superiority of yellow corn to hegari in vitamin-A content. The group of rats

dependent upon corn instead of hegari for vitamin not only produced larger litters but suckled a greater percentage of them and weaned them at a greater weight. However, it is evident that yellow corn does not provide enough vitamin A for continued rearing of offspring,

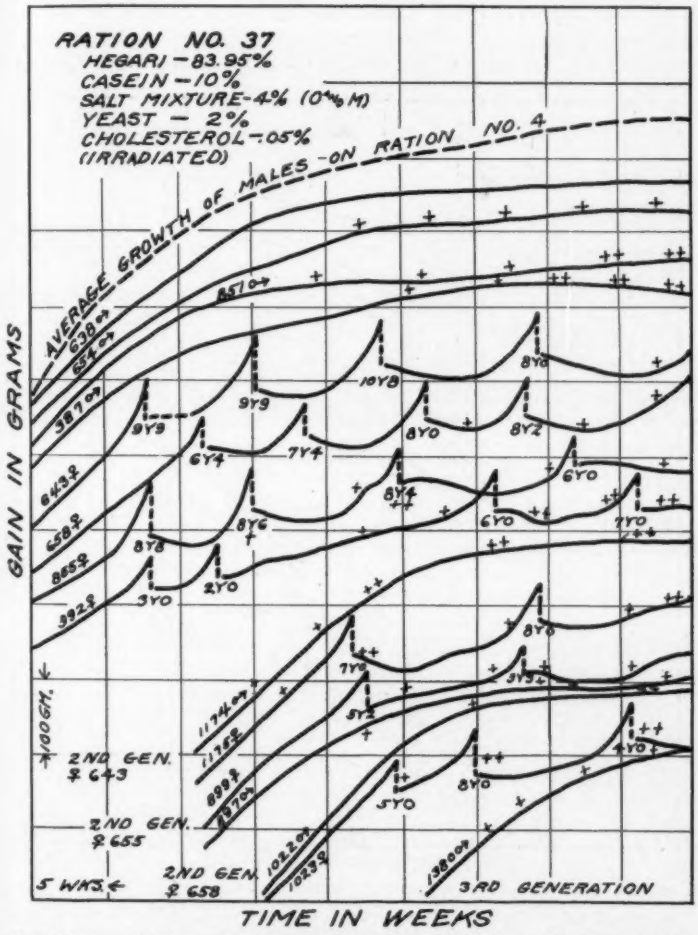

FIGURE 8.—Growth and reproduction records of representative animals receiving hegari as the chief source of vitamin A in an otherwise complete ration. None of the animals attained the rate of growth of the animals receiving additional vitamin A (note dotted curve). An early break in resistance to infection was indicated by the appearance of ophthalmia (note + signs). The females evidenced great difficulty in reproduction; they lost weight during the lactation period, and infant mortality was relatively high

as shown by the inferior reproductive records in the later generations on ration 3.

Not only are hegari and yellow corn inadequate providers of sufficient vitamin A to induce optimum growth and reproduction but

apparently neither can be depended upon even to maintain animals in good health over a long period of time. A break in health and lowered resistance to infection were demonstrated by the appearance of positive signs of ophthalmia in both groups of animals. Here again, however, the corn-fed animals were the more fortunate, ophthalmia not appearing before the eleventh month in the first generation, whereas this characteristic symptom of vitamin-A deficiency appeared as early as the fifth month among the first-generation

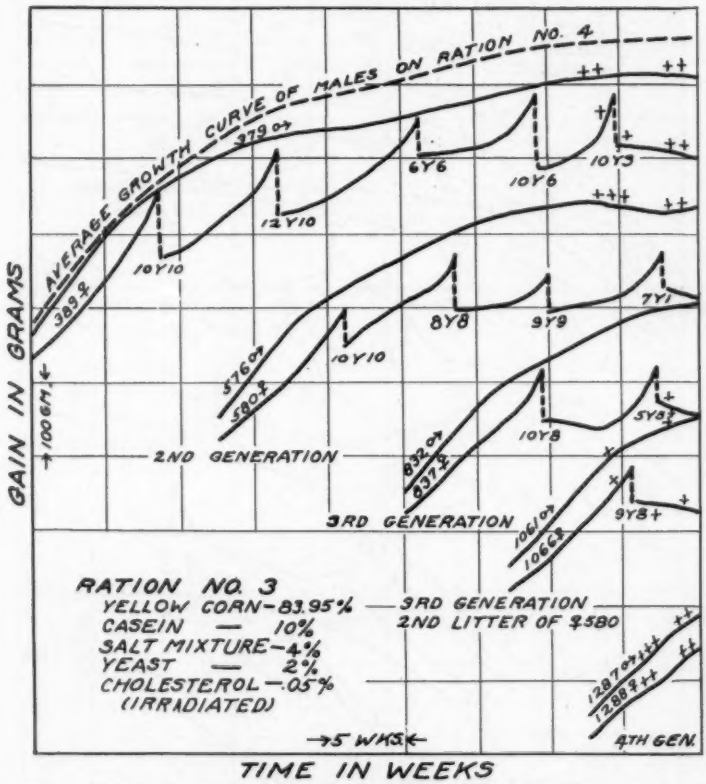

FIGURE 9.—Growth and reproduction records of representative animals receiving yellow corn as the chief source of vitamin A in an otherwise complete ration. Although these animals grew at an optimum rate at first they never attained the maximum adult size of the animals given additional vitamin A (note dotted curve). Ophthalmia (+ signs) appeared late in the first generation but earlier in each succeeding generation, and each successive generation was less capable of successful lactation

animals dependent upon hegari for their vitamin A. Indication of respiratory infection evidenced by coughing, sneezing, and nasal discharge, and premature signs of old age were common in both groups, but a higher degree of health and vigor was obtained in the group reared upon the vitamin-A-supplemented hegari ration.

All of the evidences of the inadequate vitamin-A content of the hegari and corn rations are demonstrated more forcibly in the suc-

cessive generations. Not only is the rate of gain in the young lessened, the young not reaching the optimum size for their age, but the females are less productive and success in rearing their young is greatly reduced. The indications are that the families confined to hegari for vitamin A would soon die out. The second generation

FIGURE 10.—Female No. 876, reared on ration No. 4, with her litter of seven (fourth generation) normal, healthy young at 3 weeks of age

females were slower to attain sexual maturity and succeeded in raising comparatively few of their young (2 per cent). The young were stunted in size and physically inferior in every way. Positive signs of ophthalmia occurred early in the second generation and appeared in their young (third generation) before weaning in the

FIGURE 11.—Female No. 658, reared on ration No. 37, with her third litter. Although three of her original litter of eight (second generation) were alive at 3 weeks of age they were weak, stunted and under-developed

second week, showing a low vitamin-A content of the mother's milk. This eye condition in the young before weaning usually improved somewhat when the offspring began to partake of the mother's ration.

Not only was each generation inferior to the preceding one, but each successive litter was smaller in size, more susceptible to infection,

and lower in reproductive capacity. Thus the first litter of female 855 averaged 37 gm. in weight and appeared physically fit, whereas the second litter averaged 30 gm. and showed ophthalmia at the time of weaning. In this respect also the superiority of yellow corn over hegari is unmistakable. However, though four generations of corn-fed animals were obtained during the 12 months' of experimental observation, each generation was less well equipped physically. The number of young born falls off as well as the percentage of offspring weaned, and eye infection appears earlier in each generation. Comparing corn and hegari in these respects, it is significant that the symptoms of lack of vitamin A in the fourth generation of corn-fed animals are of practically the same order as those appearing in the second generation of the hegari-fed group.

The inability of the young of each generation to develop as fully as those of the preceding generation may well be explained by the difference in the amount of vitamin A which was stored in their bodies. Vitamin A can be stored in large quantities, the amount depending upon the opportunity which the animal has for acquiring a reserve; that is, upon the concentration of vitamin A in the ration upon which the animal has fed and the length of time that it has had access to the ration (*12*, *17*). It has been shown that the concentration of vitamin A in cow's milk is directly proportional to the concentration of the vitamin in the ration upon which the mother is maintained (*1a*). Animals at weaning may, therefore, possess a considerable store of vitamin A which would enable them to undergo a subsequent lack of this vitamin with less immediate ill effects and for a longer period of time than other animals of less fortunate dietary history.

There is ample reason for believing that the original animals used in this investigation possessed at weaning a reserve of vitamin A which fortified them for some time against a lack of this vitamin in the food upon which they were subsequently fed. That there was a gradual depletion of this initial surplus in the animals fed a ration in which either corn or hegari served as the sole source of vitamin A was demonstrated by the retardation of growth and failure in health as the animals matured on rations 37 and 3, and their later inability to raise their young. Their young were born with a smaller reserve of vitamin A and they had less opportunity to acquire any considerable store from their mother's milk. At weaning time, therefore, they were on a lower nutritional plane and less prepared to withstand any lack of vitamin A in their subsequent ration. The young of each successive litter were endowed with a smaller vitamin-A surplus and in turn had less to pass on to their young.

Obviously, then, such animal-feeding experiments as are here reported will fail of correct interpretation unless the storage factor be considered and the effect of a dietary régime studied over a long period of time. That differences in results of short-time feeding experiments under different conditions are to be expected is shown by the following experiments.

Young animals taken at the time of weaning from breeding rations of different vitamin-A content obtained by varying the percentage of alfalfa meal were placed on ration 37 and the response noted and compared. All of the animals used appeared physically fit and weighed from 50 to 65 gm. at weaning.

Group A consisted of a pair of 28-day-old rats whose mother had been reared on a ration containing 3 per cent of alfalfa meal. Group B and C mothers were raised on the same breeding ration, except that it contained 5 and 10 per cent of alfalfa meal, respectively. Group D, weaned from the stock colony, was given a diet entirely devoid of vitamin A[4] for a period of four weeks, which time interval

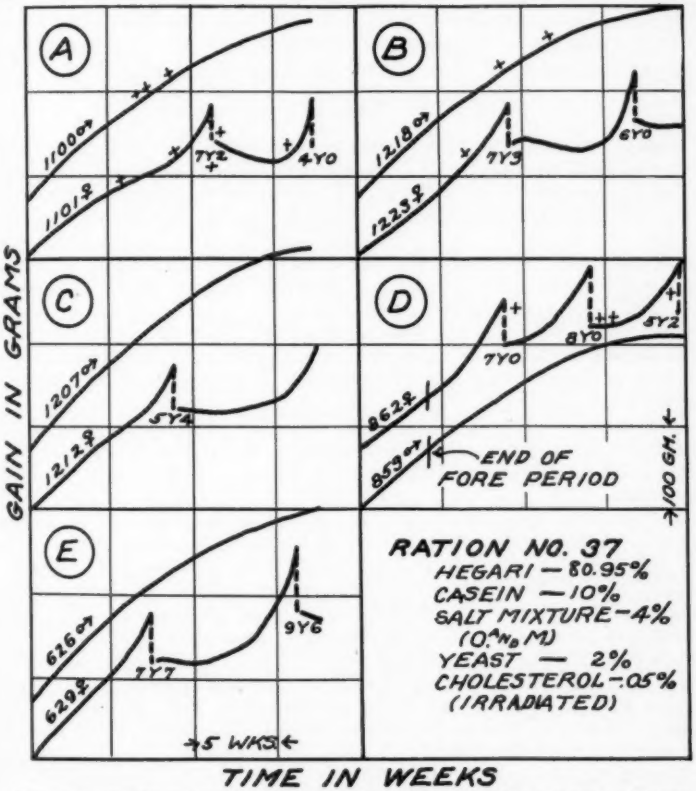

FIGURE 12.—Growth and reproduction records of animals possessing different stores of vitamin A, when placed upon a diet in which hegari served as the chief source of vitamin A. The opportunity for acquiring a reserve supply of vitamin A was least in pair A, only slightly greater in pair B, and twice as great in pair C. Pair D had their store of vitamin A exhausted before they were placed on ration 37. Pair E was taken from the stock colony at weaning and had, therefore, acquired a considerable store of vitamin A. Ophthalmia (+ sign) appears earlier and reproduction records are inferior for those animals possessing small vitamin-A reserves

has been proved many times practically to exhaust the existing vitamin-A stores in these animals. They were then confined to ration 37 in which hegari furnished all of the vitamin A. The results are shown in Figure 12.

[4] The vitamin-A-free but otherwise adequate diet used in this laboratory consists of 18 per cen textracted casein, 10 per cent dried yeast, 1 per cent NaCl, 4 per cent Osborne and Mendel's salt mixture, 66.95 per cent cornstarch, and 0.05 per cent irradiated cholesterol.

The unmistakable evidences of the inadequacy of vitamin A in ration 37 appeared earlier when the breeding rations of the animals contained less of this vitamin. Thus ophthalmia appeared in the sixth week in group A, in the eighth week in group B, and had not appeared in group C in the tenth week. Ophthalmia did not appear in the animals taken from the stock colony at weaning until the fifth month. It is again evident that hegari does not provide sufficient vitamin A for maintenance in health. If, however, the animals have an initial vitamin-A reserve, the inadequacy of the hegari ration will not be apparent until this surplus has been exhausted.

SUMMARY AND CONCLUSIONS

Comparative chemical analysis of hegari, yellow milo, and yellow corn shows the sorghums to be somewhat higher in protein and lower in fat than corn. This difference in chemical composition, however, does not satisfactorily explain the observed difference in nutritive value.

Like corn, hegari and milo when fed to rats as the sole source of nutriment do not promote normal development or even maintenance in health over a normal life span.

Like corn, hegari is inadequate in protein content. When fed to rats as the chief source of protein in an otherwise complete ration, growth is subnormal, sexual maturity delayed, and reproduction highly unsuccessful.

Like corn, hegari does not contain sufficient mineral elements to promote normal growth and reproduction and must be supplemented with sodium, chlorine, and calcium if normal nutrition is to be expected.

Yellow corn appears to be a far better source of vitamin A than hegari. Albino rats confined to a ration in which hegari served as the sole source of vitamin A in an otherwise adequate ration, grew at a fairly normal though not optimum rate and appeared to be in good health until their store of vitamin A was exhausted. The small amount of vitamin A in hegari, however, proved insufficient for continued growth at even a normal rate. All of the animals exhibited a low degree of health and vigor with pronounced susceptibility to infection and a marked failure in reproduction and rearing of their young. The indications are that families dependent on hegari for vitamin A would soon die out.

Hegari supplemented with suitable quantities of protein, mineral, and vitamin A not only promoted growth at an optimum rate and maintained the animals in every appearance of health and vigor, but also provided for the added nutritive demands of successful reproduction and lactation.

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A QUANTITATIVE COMPARISON OF THE VITAMIN-A CONTENT OF YELLOW CORN AND THE GRAIN SORGHUMS HEGARI AND YELLOW MILO[1]

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INTRODUCTION

Nutritive tests of the comparative dietary value of the sorghum grains and yellow corn carried on in the author's laboratory at the University of Arizona and presented in a previous paper[2] have demonstrated qualitatively the superiority in vitamin-A content of yellow corn to the grain sorghums hegari and yellow milo. Both hegari and yellow milo when fed to rats as the sole source of vitamin A in an otherwise complete ration were shown to be far less able than yellow corn to promote normal growth, maintenance of health and vigor, and more especially, reproduction and successful rearing of the young.

It is the purpose of this paper to compare quantitatively the vitamin-A content of yellow corn and the grain sorghums hegari and yellow-milo.[3]

METHODS AND MATERIAL

Selected samples of hegari, dwarf yellow milo, and yellow corn grown on the university experimental farms and yellow corn grown in Riley County, Kans., were used in the tests.

The experimental method employed for the quantitative measurement of the vitamin-A content of the three grains was that developed by Sherman and Munsell.[5] Young albino rats of known nutritional history[6] taken at the time of weaning (28 days) from the stock colony were placed on a vitamin-A-free but otherwise adequate ration composed of 18 per cent casein, 10 per cent dried brewer's yeast, 4 per cent Osborne and Mendel's salt mixture, 1 per cent sodium chloride, and 67 per cent cornstarch. The casein was freed from vitamin A by three successive extractions of one hour with fresh boiling 95 per cent alcohol under a reflux condenser and filtered when hot by suction.

Vitamin D was incorporated into this ration either by irradiating the cornstarch spread out in thin layers by means of an ultra-violet lamp for a period of 30 minutes at a distance of 12 inches, or by the addition of 0.05 per cent of commercial cholesterol irradiated in the same fashion.[7]

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[1] Received for publication July 24, 1929; issued June, 1930.

[2] SMITH, M. C. THE COMPARATIVE NUTRITIVE VALUE OF YELLOW CORN AND THE GRAIN SORGHUMS HEGARI AND YELLOW MILO. Jour. Agr. Research 40: 1129–1145, illus. 1930.

[3] In 1919, Steenbock [4] called attention to the association of vitamin A with yellow pigmentation and demonstrated that yellow corn is richer in vitamin A than white corn. Hegari is without yellow pigmentation but yellow milo contains pigment, located chiefly however in the epicarp.

[4] STEENBOCK, H. WHITE CORN VS. YELLOW CORN AND A PROBABLE RELATION BETWEEN THE FAT-SOLUBLE VITAMINE AND YELLOW PLANT PIGMENTS. Science (n. s.) 50: 352–353. 1919.

[5] SHERMAN, H. C., and MUNSELL, H. E. THE QUANTITATIVE DETERMINATION OF VITAMIN A. Jour. Amer. Chem. Soc. 47: 1639–1646, illus. 1925.

[6] The stock colony in this laboratory was raised on Sherman's diet B, composed of two-thirds whole wheat, one-third whole milk powder, and sodium chloride equal to 2 per cent of the weight of the wheat. Fresh lettuce was given daily.

[7] SHERMAN, H. G., and BURTIS, B. FACTORS AFFECTING THE ACCURACY OF THE QUANTITATIVE DETERMINATION OF VITAMIN A. Jour. Biol. Chem. 78: 671–680. 1928.

When the animals became practically stationary in weight on this vitamin-A-free ration (between the fourth and fifth week) and showed other indications of the exhaustion of reserve of vitamin A present in their bodies at weaning time, they were placed in individual all-metal cages with raised screen bottoms to prevent access to excreta. The basal vitamin-A-free ration and fresh distilled water were given ad libitum. Graded, weighed amounts of the ground grains whose vitamin-A content was to be measured, were fed daily for eight weeks to rats which had been carefully matched as to litter, sex, and weight. At least one, and usually two, representative animals (negative controls) were taken from each litter and kept on the unsupplemented basal ration.

All of the animals were weighed weekly and records kept of their weight and food consumption. General health observations were made daily and notations made of the time of appearance and severity of such manifestations of vitamin-A deficiency as the eye disease ophthalmia, respiratory infections evidenced by sneezing, coughing, and nasal discharge, cutaneous malnutrition, and diarrhea. At the termination of the experimental period the animals were chloroformed, autopsies performed, and records made of such post-mortem evidences of infection due to lack of vitamin A as pus in the salivary glands, middle ear, sinuses, lungs, and bladder.

Growth response to the additions of weighed amounts of the grain supplements and the time of appearance and severity of the above-mentioned symptoms of vitamin-A deficiency were used as criteria of the amount of vitamin A present in the grains under test. The results were expressed in terms of units of vitamin A,[8] a unit of vitamin A as defined by Sherman being that amount which when fed daily to a standard test animal (as prepared above) will promote an average gain of 25 gm. in 8 weeks.

EXPERIMENTAL DATA

MEASUREMENT OF VITAMIN A IN HEGARI

The results of feeding hegari in amounts of 2, 3, 4, 5, and 6 gm. as the sole source of vitamin A are given in Table 1. With the higher levels of feeding, adjustment in the basal vitamin-A-free ration was made to insure adequate protein and mineral intake, as the grains formed such a large part of the diet.

Animals taken from the stock colony at the time of weaning and given a vitamin-A-free but otherwise adequate ration were found to exhaust their store of vitamin A between the fourth and fifth week (average 33 days). When continued upon the unsupplemented vitamin-A-free ration (negative controls) there was immediate loss of weight followed by the appearance of ophthalmia, infections of the respiratory tract, cutaneous malnutrition, and often diarrhea. Death followed usually before the end of the eight weeks' experimental period in this group, the animals living on an average 36.3 days after the depletion of their vitamin-A reserves. Upon autopsy, all of the animals showed signs of severe infection in the glands at the base of the tongue and in the sinuses, middle ear, and bladder.

[8] The unit as used here has a somewhat different value than that defined by Sherman because of the fact that the average weight of the animals at the end of the fore period is greater than that of Sherman's animals.

TABLE 1.—*Summarized results of feeding various amounts of hegari daily to rats as their sole source of vitamin A*

Amount of hegari fed daily	Animals used	Average initial weight	Average weight at end of fore period	Average gain or loss in weight in 8 weeks	Probable error of mean gains or losses	Average survival in test period	Remarks
Grams	*Number*	*Grams*	*Grams*	*Grams*		*Days*	
0	31	53.9	128	−43.8	±2.2	36.3	Ante-mortem and post-mortem evidences of severe infection.
2	8	53.7	142	−19.2	±3.6	49.6	Do.
3	15	51.3	131	+7.0	±2.6	53.8	Fully 75 per cent showed both ante-mortem and post-mortem signs of infection.
4	18	52.6	133	+12.1	±2.0	55.3	50 per cent showed more than one sign of infection.
5	8	57.2	134	+22.0	±1.3	* 56.0	Slight nasal discharge only infection noted.
6	5	51.8	135	+39.0	±3.4	* 56.0	No ante-mortem or post-mortem evidences of infection.

* Survived the entire period.

Supplementing the vitamin-A-free ration with 2 gm. of hegari daily did not cause much improvement. Half of the animals in the group fed 2 gm. of hegari daily as the sole source of vitamin A died before the close of the eight weeks' experimental period and the others lost weight. All of the animals evidenced ophthalmia in some degree (from + + to + + + + +) and showed post-mortem symptoms of severe infection in at least two places, usually in the glands at the base of the tongue, sinuses, and middle ear. Except for the fact that more of these animals lived throughout the eight weeks of the experimental period and lost less weight, the results were little better than those obtained from the negative control animals.

Although approximately 25 per cent of the animals receiving 3 gm. of hegari daily in addition to the basal vitamin-A-free ration died before the end of the eight weeks' experimental period, an average gain in weight of 7 gm. was observed in this group. Fully three-fourths of the animals, however, showed both ante-mortem and post-mortem signs of severe infection. Apparently, 3 gm. of hegari fed daily does not furnish sufficient vitamin A to insure even a limited rate of growth or freedom from the severe infections which result from a lack of vitamin A.

Four grams of hegari fed daily as the only source of vitamin A in an otherwise complete ration permitted all but two of the animals to live throughout the test period. Although an average gain in weight of 12.1 gm. was recorded for this group, fully three-fourths of the animals had ophthalmia in some degree, and more than half of them showed at least two post-mortem evidences of infection, that of the bladder being relatively more frequent.

All the animals receiving 5 gm. of hegari daily lived the eight weeks' period and made an average gain of 22 gm. A small loss in weight in the last week of the period was noted, however. No severe signs of infection were observed either before or after death, though in 33 per cent of the cases there was noted a more than usual amount of thick mucus in the nasal passages. It would appear that 5 gm. of hegari fed daily contains slightly less than the amount of vitamin A necessary to insure the unit rate of gain in the standard test animal and give complete protection against infection.

Feeding hegari as the only source of vitamin A at the level of 6 gm. daily sufficed to induce an average gain in weight of 39 gm. in the experimental eight weeks' period. None of the animals showed infection of any kind nor any indication of insufficiency of vitamin A other than subnormal growth. Obviously 6 gm. of hegari contains more than one unit of vitamin A, as defined by Sherman.

Table 1 summarizes the data obtained by feeding graded amounts of hegari as the sole source of vitamin A in an otherwise complete diet. These same data are depicted graphically in Figure 1.

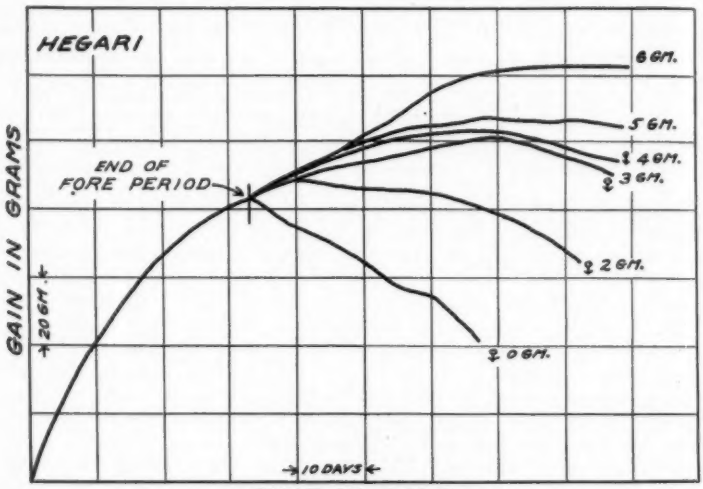

FIGURE 1.—Average gain curves of rats receiving various amounts of hegari daily as the sole source of vitamin A for a period of eight weeks

Obviously the unit [3] rate of gain lies somewhere between that induced by feeding 5 and 6 gm. of hegari, respectively, as the only source of vitamin A in an otherwise adequate diet.

MEASUREMENT OF VITAMIN A IN YELLOW MILO

The results of feeding yellow milo as the sole source of vitamin A in amounts of 1, 1.5, 2, 2.5, 3, and 4 gm. appear in Table 2. The same data are presented graphically in Figure 2.

All of the animals fed only 1 gm. of yellow milo as a daily supplement to a vitamin-A-free, though otherwise adequate, diet lost weight (average 29.5 gm.), evidenced ophthalmia (+ + + +) before death, and showed extreme signs of infection upon autopsy. A slightly longer survival than the negative controls and less loss in weight are the only indications that the rats received any vitamin A.

The animals fed 1.5 gm. of milo daily survived considerably longer than those receiving no addition to their vitamin-A-free ration. However, 1.5 gm. of yellow milo did not prevent any of the animals in this group from dying as a result of lack of vitamin A. Ante-mortem and post-mortem symptoms of severe infection were present in every case.

[3] The unit as used here has a somewhat different value than that defined by Sherman because of the fact that the average weight of the animals at the end of the fore period is greater than that of Sherman's animals.

TABLE 2.—*Summarized results of feeding various amounts of yellow milo daily to rats as their sole source of vitamin A*

Amount of milo fed daily	Animals used	Average initial weight	Average weight at end of fore-period	Average gain or loss in weight in 8 weeks	Probable error of mean gains or losses	Average survival in test	Remarks
Grams	*Number*	*Grams*	*Grams*	*Grams*		*Days*	
0	31	53.9	128.0	−43.8	±2.2	36.3	Ante-mortem and post-mortem evidences of severe infection in all animals.
1.0	4	61.5	151.2	−29.5	±5.7	48.0	Survival prolonged but animals were all severely infected.
1.5	7	59.8	133.0	−11.4	±2.8	50.5	Do.
2.0	15	54.2	131.8	+11.4	±2.6	52.8	25 per cent died during test period. 66 per cent of all animals had ophthalmia and pus sacks in tongue glands.
2.5	6	50.1	113.5	+21.6	±2.6	*56.0	Only one animal in this group had ophthalmia (+); no other sign of infection.
3.0	6	45.1	131.1	+28.5	±1.1	*56.0	No ante-mortem or post-mortem evidences of infections.
4.0	7	52.1	138.0	+43.7	±2.0	*56.0	Do.

* Survived the entire period.

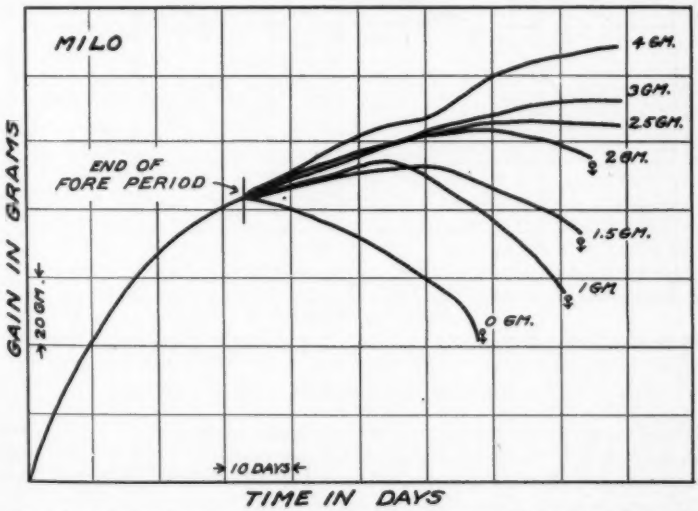

FIGURE 2.—Average gain curves of rats receiving various amounts of yellow milo daily as the sole source of vitamin A for a period of eight weeks

Two-thirds of the animals in the group fed 2 gm. of yellow milo daily in addition to their vitamin-A-free ration lived the eight weeks' of the experimental period, though they grew slowly. An average gain of 11.4 gm. in the test period was obtained. Sixty-six per cent of them, however, had infection resulting from insufficient vitamin A in their food.

Two and one-half grams of yellow milo fed daily furnishes sufficient vitamin A to induce an average rate of gain in the test animals of 21.6 gm. Most of the rats in this group were free from infection in those parts of the body which are commonly unable to resist the

invasion of bacteria in the absence of vitamin A in the ration. One rat, however, showed definite signs of ophthalmia in the last of the experimental period.

Three grams of yellow milo fed daily as the sole source of vitamin A not only induced an average rate of gain of 28.5 gm. in the eight weeks' experimental period, but also insured complete protection against infection in all of the animals.

An average gain of 4.37 gm. was obtained when 4 gm. of milo was fed daily to the standard test animals. No symptoms of vitamin-A deficiency were evident in this group.

From the results of these experiments it is apparent that slightly more than 2.5 gm. of dwarf yellow milo contain 1 unit of vitamin A.

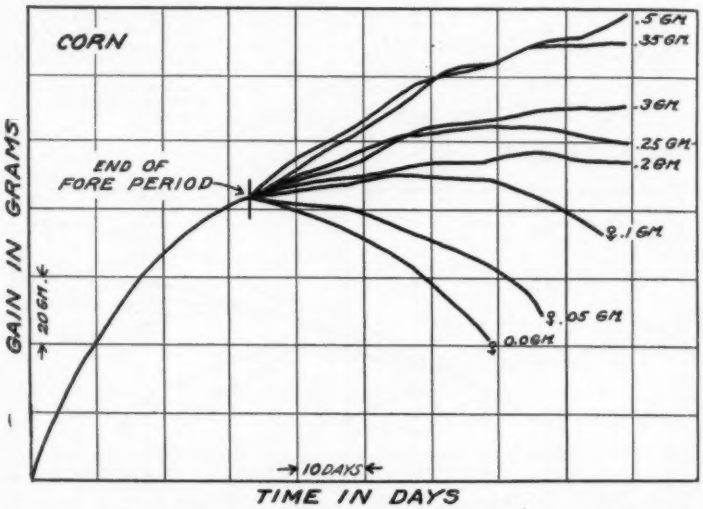

FIGURE 3.—Average gain curves of rats receiving various amounts of yellow corn daily as the sole source of vitamin A for period of eight weeks.

MEASUREMENT OF VITAMIN A IN YELLOW CORN

Results of feeding yellow corn in graded amounts of 0.05, 0.1, 0.2, 0.25, 0.3, 0.35, and 0.5 gm. as a daily supplement to a diet which contained no other source of vitamin A are presented in Table 3 and Figure 3.

Yellow corn fed daily in the amount of 0.05 gm. does not provide enough vitamin A to permit the standard test animals, which have no reserves of vitamin A, to live the experimental eight weeks' period. Every rat had ophthalmia (+ + to + + + +) by the fifth week and upon autopsy showed signs of infection of the same order as the negative control animals.

The animals fed 0.1 gm. of yellow corn daily lived longer than the negative controls (average 53.5 days), but they were not able to maintain themselves in health. Loss of weight occurred after the third week of the test period and marked susceptibility to infection followed in every case.

TABLE 3.—*Summarized results of feeding various amounts of yellow corn daily to rats as their sole source of vitamin A*

Amount of corn fed daily	Animals used	Average initial weight	Average weight at end of fore period	Average gain or loss in weight in 8 weeks	Probable error of mean gains or losses	Average survival in test period	Remarks
Grams	*Number*	*Grams*	*Grams*	*Grams*		*Days*	
0	31	53.9	128.0	−43.8	±2.2	36.3	Ante-mortem and post-mortem evidences of severe infection in all animals.
.05	8	49.8	131.5	−35.2	±2.6	43.0	Do.
.10	6	50.0	140.1	−10.3	±4.1	53.5	75 per cent of the animals showed both ante-mortem and post-mortem signs of infection.
.20	4	58.2	137.0	+11.2	±0.8	* 56.0	Definite though mild ophthalmia in 33 per cent of the animals.
.25	9	51.0	139.2	+17.1	±2.2	* 56.0	No ante-mortem or post-mortem evidences of infection.
.30	5	54.2	125.2	+27.6	±1.4	* 56.0	Do.
.35	2	58.0	136.0	+46.0	±2.0	* 56.0	Do.
.50	2	42.0	120.0	+53.5	±3.0	* 56.0	Do.

* Survived the entire period.

When 0.2 gm. of yellow corn was fed daily to rats as the only source of vitamin A in an otherwise adequate ration, a limited rate of gain (11.2 gm. in eight weeks) was made. It was not sufficient, however, to prevent a loss in weight after the sixth week or to insure the animal against infection, for more than 50 per cent of the animals in this group had definite though mild ophthalmia and pus in the glands at the base of the tongue.

The feeding of yellow corn at the level of 0.25 gm. daily induced an average rate of gain of 17.1 gm. in the eight weeks' test period. However, the initial rate of gain was not maintained throughout the whole experimental period and 33 per cent of the animals had definite though not severe (+) ophthalmia in the last week. Considerable variation in growth response was obtained in this group, as is to be expected when slightly less than one unit of vitamin A is fed daily.

Yellow corn fed at the level of 0.3 gm. daily or greater induced a definite rate of gain. Resistance to infection was relatively high, for in no case was ophthalmia or any post-mortem symptom of infection due to the lack of vitamin A evident.

An inspection of Table 2 shows that practically a unit of vitamin A is contained in 0.3 gm. of high grade yellow corn. Feeding yellow corn in this amount daily as the sole source of vitamin A resulted in a unit rate of gain in the test animals and freedom from infection.

From the results here reported it is apparent that yellow corn is a far better source of vitamin A than either hegari or yellow milo. It is evident also that yellow milo, contains more of this vitamin than hegari. The unit rate of gain (25 gm. in eight weeks) was induced by feeding slightly less than 0.3 gm. of yellow corn, 3 gm. of yellow milo, and somewhat more than 5 gm. of hegari. Practically the same rate of gain (11 gm.) in the test period was also obtained by feeding 0.2 gm. of yellow corn, 2 gm. of milo, and 4 gm. of hegari.

CONCLUSIONS

From the data obtained upon the quantitative measurement of the vitamin-A content of yellow corn and the sorghum grains hegari and yellow milo it may be concluded that the yellow milo is twice as rich in vitamin A as hegari, and that yellow corn is practically 20 times as rich a source of vitamin A as hegari.

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